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A WHITE SPRUCE OUTLIER AT SHUSHAN, NEW YORK

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White spruce (*Picea glauca* (Moench) Voss) is one of the most widely distributed conifers in North America, occurring in a broad band from the Atlantic coast to Alaska and northward to the limit of trees. Its southern boundary is irregular and the factors that influence its position are imperfectly understood. In New York State, the tree is uncommon and its southern limits are marked by a scattering of small stands persisting in especially favorable ecological niches, often widely separated from one another and from the areas of more general abundance, as is often the case with relic species.

In New York, certain ecological factors seem to be common to these white spruce outliers. Lime is available from underlying bedrock, from the soil itself, from alkaline seepage or from flooding by alkaline waters. Relatively higher humidities and lower temperatures are maintained by location in intermontane valleys, by proximity to bodies of water or from seepage and evaporation. Temperatures—either maximum or minimum—do not appear to be limiting factors.

One of the most interesting of these southern stands is the Shushan Outlier, situated in southern Washington County, New York, at latitude 43° 04′ North. Ecologically, it is of special significance because of the sharp boundaries and marked floristic differences between this isolated boreal community and the surrounding deciduous and pine woodlands, transitional from the southern oak-chesnut to the northern hardwood forest.

The first botanist to recognize and report the occurrence of white spruce in Eldridge Swamp, at the great bend where the Batten Kill turns from southwest to north two miles south of Shushan was Frank Dobbin (1873-1950), a native of Shushan and an enthusiastic and thoroughly competent amateur botanist. In 1912, State Botanist C. H. Peck (1914) reported as follows:

"*Picea canadensis* (Mill) B.S.P.

Cambridge Waterworks swamp, Washington co. July. F. Dobbin and S. H. Burnham. This swamp is a large one, covering an area of approximately one square mile and the stream flowing through it is fed by cold springs which probably aid in making it a suitable habitat for this northern cold-loving spruce. This is doubtless the southern limit for it in our State and an outlying station in which it has been able to maintain itself by reason of the cold character of the soil. Nevertheless, the shortness of the leaves of these specimens indicate that its environment here is not favorable to its most vigorous development. Still it bears cones though not of large size."

(Burnham was a close friend of Dobbin's and at the time was employed by the State Museum, to which Dobbin was regularly sending specimens.)

Peck's statement is an excellent one but it does not attempt to explain why this swamp contains white spruce while scores of other comparable ones across New York, equally cold and wet, are inhabited by black spruce (*Picea mariana*). The observation that the cones are "not of large size" is well taken, for this population of white spruce —like those of certain other southern outliers— bears cones considerably smaller than those from the area of greatest abundance, around Lake Placid. Unfortunately, Peck did not present a list of associated species.

Since 1951, we have been assembling data on the natural distribution of white spruce in New York and it was while checking Dobbin's seem-

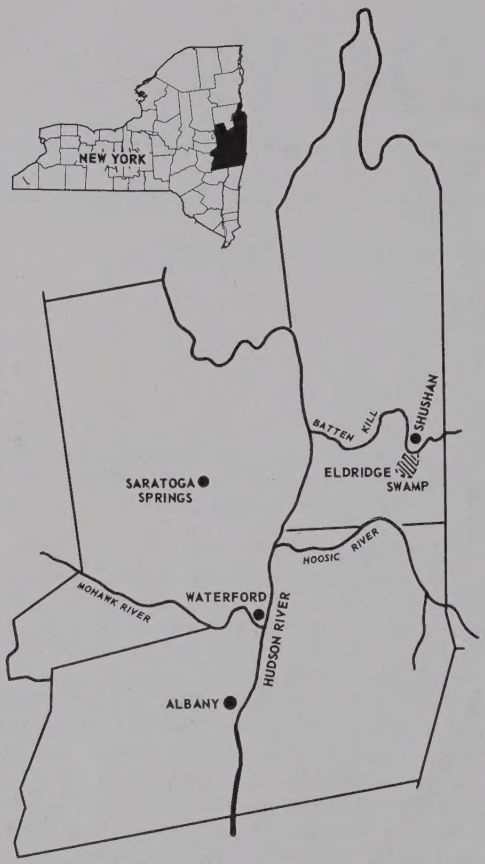

FIG. 1. Map showing the location of Eldridge Swamp and its relation to nearby geographic features.

ingly unlikely record that we re-determined the location and boundaries of this outlier of boreal forest dominated by white spruce, balsam fir (*Abies balsamea*) and tamarack (*Larix laricina*). A number of field trips into the swamp have provided opportunity for collection and observation. In July, 1957, the Eastern New York Botanical Club conducted a foray there, which considerably increased our knowledge of the lesser flora. Erwin L. Annis, in charge of the Cambridge Hatchery, has provided us with the data on the depth of the organic layer in the swamp and has on occasion acted as guide.

The pre-glacial drainage of the Shushan area was through a number of deep valleys running southwest and south into the Hoosic, a main eastern tributary of the Hudson. During the late Pleistocene, these valleys were obstructed by masses of stagnant ice. The one south of Shushan was big enough to dam the Batten Kill, ponding its waters in the valley to the west, whence it cut through a low divide to develop its present course westward into the Hudson. Over and against the ice mass in the wide valley that extends from the present great bend south to the Hoosic, the Batten Kill built a gravel plain, in which was buried the mile-square mass of ice whose ablation left the ice-bloc hole now known as Eldridge Swamp. The ice and water-born material that surrounds the depression derives from the rocks of southwestern Vermont, many of which are calcareous. Along the south and southwest margins of the swamp, the slopes from the level of the gravel plain are short and steep; on east and west they are irregular; while on the north the border tapers off into the gravel bars built by the Batten Kill. The elevation of 460 feet, at the eastern edge of the broad Hudson Valley makes this a lowland site, even though there are mountains close by to the east.

In the wettest, southern part of the swamp, the ground surface is covered with hummocks of living and dead woody material, between which are shallow pools of open water and soft muck. In February, 1958, when the swamp was frozen hard, Annis made soundings along the open streams to determine the depth of the organic layer, using an 8-foot wooden pole. These probing stations are shown by number on Figure 2.

TABLE I. Depth to refusal of the muck layer. Eldridge Swamp, Shushan, New York. 1958

Station 1	24 inches
2	42 "
3	34 "
4	33 "
5	Greater than 96 "
6	42 "
7	Greater than 96 "
8	42 "

Annis thinks that depths at Stations 5 and 7 may actually be of the magnitude of twenty feet and that similar depths occur in the area south of the Waterworks outlet.

The climate of this part of New York is modified continental, with cold winters, hot summers and wide and rapid fluctuations in temperature. The weather station nearest Eldridge Swamp is at Greenwich, eight miles west and at 425 feet elevation. Table 2 indicates the salient features of the climate there.

Eldridge Swamp derives its water from two sources. Each spring, it is completely inundated by high water from the Batten Kill whose banks

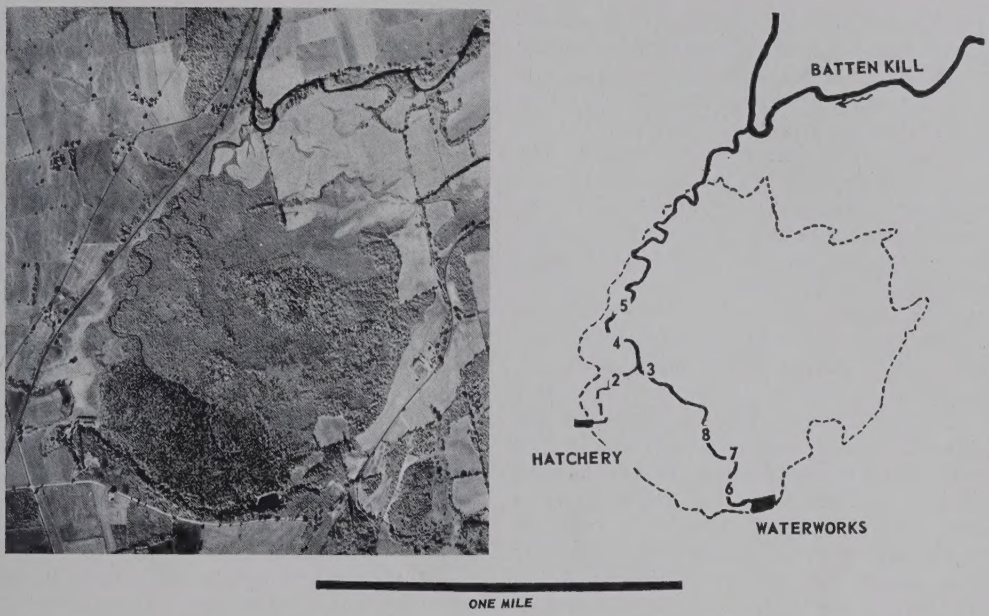

FIG. 2. Aerial photo (left) of Eldridge Swamp (September 29, 1948) taken before the Great Wind of 1950. The dark area in the southern part is the forest dominated by white spruce. The numbers on the overlay (right) indicate the stations where the depth of the muck was measured.

are somewhat higher than the level of the swamp. A substantial portion of this freshet is ponded, to be lost by evaporation and transpiration and by slow outward flow through the meandering outlet stream. From the south, the swamp is continually watered by a series of springs coming out of the foot of the gravel plain along the ancient ice contact line. One of these supplies the Cambridge Waterworks, another the Conservation Department's Cambridge Fish Hatchery. Others are used as sources of water for potato spraying. All

TABLE II. Climatic data for Greenwich, New York, from Mordoff (1949)

Temperature	
Mean for February (coldest month)	18.9°F
Mean for July (warmest month)	70.7°F
Mean annual	46.0°F
Lowest	−28° F
Highest	99° F
Length of growing season	147 days
Annual precipitation	35.77″
Annual snowfall	47.90″

provide clear, hard water. At the hatchery, the pH is 7.7 while that of the Batten Kill twelve miles below the swamp is 7.8; for eastern New York, these values are high. As can be seen in Figure 2, the outlet stream meanders west and then north into the Batten Kill. The Owl Kill, which drains the higher land to the west and south of the swamp and which flows south into the Hoosic River is a small, underfit stream in a wide, ancient valley.

With the ablation of the Cary ice, some fourteen thousand years ago (Suess 1956) the same association of boreal species that was colonizing newly deglaciated land further west in New York seems also to have invaded this area and probably did so as soon as the soil mantle over the ice blocks thawed to sufficient depth to permit the establishment of tree seedlings. Pollen profiles from central New York (McCulloch 1939, Cox 1958) indicate that this forest was composed of spruce (probably white spruce), balsam fir and pine. Other present members of this association—tamarack and balsam poplar (*Populus balsamifera*)—have pollen which does not fossilize well and so are presumed to be under-represented in the spectra.

That white spruce was once more widely distributed in the middle Hudson Valley is attested by two Pleistocene records of well-preserved cones from Waterford (Clarke 1910) and Saratoga (Eliason 1958). See Fig. 1.

Original land survey records, although they do not specifically indicate the presence of white spruce, do record the general nature of the primeval forests of this area. Only the surveys covering the western edge of Eldridge Swamp are now

known (Campbell 1768). One corner was marked on a red maple (*Acer rubrum*) "in a sunken swamp or fly." On the drier sites on the gravel plain to the south, the timber was oak (*Quercus alba, Q. rubra, Q. velutina*), chestnut (*Castanea dentata*) and white pine (*Pinus strobus*). The presence of "pine plains" on the site of Cambridge indicates occasional violent disturbance of the forest, as by windfall and fire. Areas of beech, sugar maple and hemlock occurred on the cooler slopes of the surrounding hills.

From interviews with local people, it appears that white spruce originally occurred over much of the poorly drained area but mostly south and east of the outlet streams, as indicated by the dark area (Fig. 2), although scattered trees did and still do occur further north in the swamp. To the north and northeast, farming and grazing have encroached upon the drier, drainable portions so that the swamp border is indistinct. Until recently, the largest remaining body of spruce timber stood in the southeast corner. Much of this was blown down by the Great Wind of 1950. Subsequent salvage operations (1951-1954) removed not only the blowdown but also most of the remaining merchantable timber. Therefore, data on the original composition and size ranges of this stand cannot now be obtained. But some of the bigger spruces were in the 20" dbh class, indicating that they were old trees, if not remnants of the original forest.

The present flora of Eldridge Swamp is made up of an overstory of trees of the boreal forest (*Picea glauca, Abies balsamea, Larix laricina, Populus balsamifera*) plus components more typical of the northern hardwood forest (*Fraxinus nigra, Betula allegheniensis, B. papyrifera*) with an admixture of species adapted to a wide range of sites (*Pinus strobus, Tsuga canadensis, Populus grandidentata, P. tremuloides, Ulmus americana, Acer rubra, Thuya occidentalis* and *Salix* spp.) The shrub layer consists of northern elements (*Nemopanthus mucronata, Potentilla fruticosa, Alnus rugosa, Rhamnus alnifolia*) and those of more southern affinity (*Rhus vernix, R. radicans, Rhododendron nudiflorum, Lyonia ligustrina, Parthenocissus quinquefolia, Vaccinium corymbosum*). Among these, perhaps the most conspicuous is poison sumac, a swamp shrub of rather scattered distribution and a definitely southern range. This species still persists in the boggy areas around Saratoga, lending support to the thought that a forest not unlike that of Eldridge Swamp may have occupied that area in the not-too-remote past. Herbs include *Typha latifolia, Clintonia borealis, Lobelia spicata, Arisaema triphyllum, Symplocarpus foetidus, Malaxis brachypoda, Osmunda regalis, Caltha palustris, Coptis trifolia, Veratrum viride, Glyceira grandis, Saxafraga pennsylvanica* and *Mitella nuda. Sphagnum* occurs very sparingly, whereas *Mnium* and *Thuidium* are frequent.

On the gravel plain, the woodland remnants are composed of *Quercus velutina, Q. rubra, Q. alba, Betula populifolia* and *Populus tremuloides,* with a scattering of such shrubs as *Spirea tomentosa, Comptonia peregrina* and *Lyonia ligustrina.* The flora of the slope between swamp and gravel plain is a mixture of the more aggressive elements of the adjacent associations, invading abandoned pastureland.

Even here in Eldridge Swamp, at the extreme south edge of its range, white spruce reproduces aggressively. In the swamp proper, trees of all sizes are—or were—present, from the mature remnants of the older stands to seedlings coming up on areas exposed by recent logging. On the swamp margins, it is vigorously invading both active and abandoned pasture. An occasional tree is to be found even on the gravel plain. Half a mile to the southwest, at a location marked on Campbell's map of 1768 as the site of an "old bever pond," is an area which has been cleared, ditched and reduced to pasture. White spruce and white pine have seeded in and now dominate not only the moister portion along the ditch but have spread west into the drier upland pasture. Many of the white spruce are taller than the weeviled white pine, with heights to forty feet and diameters to twelve inches; the oldest are estimated at forty years, based on counts of internodes. They seem to have seeded in from trees in an adjacent dooryard, which are of large size and presumed to have been dug from the wild. The presence and vigor of this reproduction indicates not only the suitability of this site to its ecological requirements but also the aggressiveness of white spruce, even in competition with such a fast-growing species as white pine, provided hardwoods are kept down, as by grazing.

The flora of the Shushan Outlier—the southern segment of Eldridge Swamp—constitutes a relic boreal community dominated by white spruce, tamarack, balsam fir and balsam poplar, now almost lost in a vast expanse of more xerophytic types dominated by white pine and oaks. White spruce, the most adaptable and aggressive species, reproduces readily on suitable sites, both within and beyond the swamp. In a relatively warm climate with no more than average rainfall, this mesophytic community persists in spite of agricultural invasion and recent logging. The ecological

factors that favor its continuance are an abundance of cold alkaline water, producing a microclimate characterized by lowered temperature, higher humidity, abundant moisture and a relatively high pH.

References

Campbell, Archibald. 1768. A field book of the allotment of the patent called Cambridge. N.Y. Dept. Public Works Field Book **40**: 392-432. (ms)

Clarke, J. M. 1910. Sixth report of the Director. N.Y. Museum Bulletin **140**. Albany.

Cox, D. D. 1958. Some post-glacial forests in central and eastern New York. Unpublished manuscript.

Eliason, E. J. 1958. Personal correspondence.

McColluch, W. F. 1939. A postglacial forest in central New York. Ecology **20**: 264-271.

Mordoff, R. A. 1949. The climate of New York State. Cornell Bulletin **764**. Ithaca.

Peck, C. H. 1914. Report of the State Botanist 1912. N.Y. State Museum Bulletin **167**. Albany.

Suess, H. E. 1956. Absolute chronology of the last glaciation. Science **123**: 355-357.

THE NUTRIENT STATUS OF THE SOILS OF SOME NATURAL PLANT COMMUNITIES ON THE SOUTHERN TABLELANDS OF NEW SOUTH WALES

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Introduction

It has frequently been stated or implied that vegetation provides a measure of the environment, or may be used as an indicator of total environment. In view of the complexity of the factors involved, it is not surprising that relatively little experimental work has been attempted to determine the environmental factors associated with particular plant communities, or to determine the tolerance limits of individual species. Clements' (1928, 1936) concept of the climatic climax emphasized the overriding importance of climate in the distribution of vegetation, while other environmental factors were considered to be of only secondary importance. In the United States the general acceptance of Clements' concept focussed attention on climate, and the effects of other environmental factors were to a large extent neglected. More recently (e.g. Jenny 1941; Major 1951; Crocker 1952; Whittaker 1953; Gorham 1955) there has been an increasing tendency to regard environmental factors other than climate as of equal importance in the delimitation of plant communities within a climatic region, and it is considered that convergence of vegetation on different sites towards a climatic climax will not always occur.

In Britain and Europe Clements' concept of the monoclimax has never been accepted (e.g. Tansley 1920, 1935, 1939; Du Rietz 1932), and the climax communities have been regarded as the result of a complexity of environmental factors, of which climate is only one.

A number of workers have reported correlations between certain edaphic factors and the vegetation. These investigations differ in the number of individual factors examined and measured, and it would appear that there has been a tendency to reach conclusions which may be correct, but which are scarcely justified by the data presented, especially when the work is confined to the investigation of only a few factors. The fact that a correlation between plant community and a soil factor can be established does not necessarily indicate that the factor in question is primarily responsible for the occurrence of the particular community on the particular site. The necessity for considering the whole environment, and of considering each factor of the environment in relation to all the others, has been stressed by Cain (1944) and by Billings (1952). These two authors regard the environment (which includes the vegetation) as holocoenotic. Jenny (1941) and Major (1951) have dealt with the same problem from a more quantitative point of view (at least theoretically), by considering the soil and vegetation as functions of a number of groups of factors. The mathematical differentiation and integration of these factors shows the complexity of the problem and the interrelations of the variables, just as did the diagram of their relationships as presented by Billings (1952).

Jenny (1941) pointed out that if soils are functions of five or more groups of factors, a universal correlation between two soil properties would not be expected. Major (1951) applied

this same argument to vegetation, and rightly concluded that universal correlations between soils and vegetation do not ordinarily exist. However, as Crocker (1952) has pointed out, it is reasonable to seek regional correlations between soil and vegetation, and such correlations are of value provided that the soils have not been influenced by the current vegetation during their lifetime. It is quite possible that under these conditions plant distribution, and hence the delimitation of plant communities, may be influenced, and even determined, by one or more soil properties.

In Britain and Europe there have been many investigations involving soil-plant relationships, perhaps especially in connection with the relationships of plants to soil pH, and to calcareous and non-calcareous soils. This literature has been discussed and reviewed by Braun-Blanquet (1951) and also recently by Krause (1958) and by Ellenberg (1958). Bach (1950) and Moor (1952, 1952a) have studied the distribution of the associations of the Alliance *Fagion sylvaticae* of the Jura of Switzerland in relation to soils, altitude and aspect. The former author concluded that on the humus carbonate and rendzina soils the development of these associations is governed by local climate, soil climate, and the mobility of the soil particles. On these calcareous soils, chemical differences are not significant in the development of different associations. He also considered that compensating factors result in one association occurring on habitats which are not identical except in their effects on the vegetation. Moor (1952, 1952a) described the different associations of the beech forests, all of which occur on limestone strata, and related them to soils, topography, altitude and aspect.

In the Cranberry Lake Region of the Adirondack Mountains, variations in the vegetation are associated with measurable soil differences (Young 1934). Allard (1942) considered that normal succession on certain areas on Bull Run Mountain in Virginia was prevented because of phosphorus deficiency in the soil. Billings (1950) studied the soils of chemically altered rocks of the Western Great Basin, and showed that they were strongly acid, and deficient in phosphorus, nitrogen and exchangeable cations. He concluded that pine stands on these soils have remained within the sagebrush zone because of the inability of the latter species to invade these mineral deficient soils. In the Sydney district of New South Wales, different types of vegetation are associated with different amounts of available phosphorus in the soils (Beadle 1954). Rain forest occurs on the soils of highest phosphorus content, while the soils of the Hawkesbury Sandstone, with a very low content of available phosphorus, support a sclerophyllous scrub forest with a high degree of xeromorphism.

Coaldrake and Haydock (1958) attempted to correlate total soil phosphorus with the distribution of natural communities in southeastern Queensland. They concluded that there was no correlation between soil phosphate and the distribution of the natural plant communities in the area studied. It is, however, unlikely that any vegetal pattern could be satisfactorily superimposed on data for total soil phosphorus obtained by chemical analysis of soil samples collected on a grid system. The analytical method used is not likely to be related to the plants' requirements or ability to absorb phosphorus. Further, to obtain a valid correlation between any soil property and the vegetation associated with it, it is surely necessary to sample the soils from within the community or communities being studied, and to test the reaction of the plants to variations in the soil property. The method used by Coaldrake and Haydock (1958) had no greater chance of success than did that of Gates *et al.* (1956). These latter authors made a somewhat detailed study of the soils of the salt deserts of Utah. They were able to show significant differences between soils, but no species was restricted in distribution by a narrow tolerance range for any specific soil factor measured. Again a study of soil-plant relationships should be based on the reactions of plants, not on chemical and physical analyses of the soils.

In the Southwestern Missouri Ozarks the development of forest and glade types of vegetation is physiographically associated with differing geologic formations (Kucera and Martin 1957). Variable composition of the parent rock and differences in rate of weathering have produced soils with different characteristics. The shallow soils of the glades have poor water relations, while those supporting forest growth have weathered to a greater depth and are more retentive of water.

One of the most striking examples of edaphic restriction is that of the serpentine soils, which have been investigated in some detail by Vlamis and Jenny (1948), Vlamis (1949), Kruckeberg (1951, 1954), Walker (1954), and Whittaker (1954). Vlamis (1949) showed that the limitation of growth on the serpentine soils is associated with the degree of calcium saturation of the soil, rather than with a low calcium-magnesium ratio. He also demonstrated deficiencies of nitrogen, phosphorus, and potassium in the serpentine

soils. The principal adaptation of plants for growth on the serpentine soils of California appears to be tolerance of low percentage of exchangeable calcium, but as Whittaker (1954) has pointed out, other environmental factors and ecotypic variation also determine the structure and floristic composition of the serpentine communities in different parts of the world.

Habitat studies in relation to floristic composition and structure of plant communities provide valuable basic information, but these must eventually be supplemented by studies of the tolerances of individual species and races, such as have been reported by Kruckeberg (1951) and McMillan (1956), and by studies of plants competing with one another (Ellenberg 1953; Knapp 1954; Moore 1959).

Over large areas of Australia, the dominants in the plant communities are various species of *Eucalyptus,* and it is frequently found that the distribution of the different species within a climatic zone appears to be related to the distribution of the soils. In the Southastern Riverina, *E. albens* woodland occurs on the red and yellow podzolics, *E. woollsiana* woodland on the red brown earths, and *Acacia pendula—Atriplex nummularia* shrub woodland on the grey and brown soils of heavy texture (Moore 1953). The sharpness of the boundaries between the communities is generally associated with the sharpness of the soil change. Sometimes specific soil properties are known to be associated with particular communities. The soils of the heath communities of Southeastern South Australia are characteristically of low fertility, with deficiencies of nitrogen, phosphorus, potassium, copper, zinc and molybdenum (Coaldrake 1951, Specht and Rayson 1957), while Beadle (1954) has correlated structure and floristic composition with the level of available phosphorus in the soil.

On the Southern Tablelands of New South Wales, there is evidence that the distribution of some communities, especially at the higher elevations, is associated with local climate (Moore 1956). However, there are many examples of abrupt change in plant community where climate does not appear to be the determining factor, and an examination of the soils may be expected to throw some light on the reasons underlying the distribution of the communities.

This paper reports the results of a study of the nutrient status of the soils of a number of plant communities occuring commonly on the Southern Tablelands of New South Wales. Clearly this is only one aspect of the soil conditions which may influence the plants growing on them, and others have yet to be determined. The results of the present study not only define more accurately the environments studied, but also provide some evidence as to the value of the natural communities as indicators of fertilizer requirements for crop and pasture production.

The community pairs selected are commonly found as adjoining communities with sharp boundaries or narrow ecotones. The sampling sites were chosen to include a range of soil parent materials, and to insure, as far as possible, that the soils of each community sampled at a particular site were formed on the same or similar parent materials.

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The Plant Communities[1] and Soils

Four plant communities commonly occurring on the Southern Tablelands were selected, viz. The *Eucalyptus rossii* Association (Dry Sclerophyll Forest, *E. macrorrhyncha—E. rossii* Alliance); the *E. melliodora—E. blakelyi* Association (Savannah Woodland, *E. melliodora—E. blakelyi* Alliance); the *E. pauciflora—E. rubida* Association (Savannah Woodland, *E. pauciflora—E. stellulata* Alliance) and the *Poa caespitosa* Association (Sod Tussock Grassland, *Poa caespitosa—Danthonia nudiflora* Alliance). The first three communities have been described for the Monaro Region and for the Australian Capital Territory respectively by Costin (1954) and Pryor (1939), and the fourth by Costin (1954) for the Monaro Region.

The *Eucalyptus rossii* Association is widespread in the Southern Tablelands and Monaro Regions of New South Wales (Pryor 1939; Costin 1954), and also extends on to the Southwest Slopes and the eastern Riverina (Moore 1953). It occurs commonly on shallow skeletal soils derived from various parent materials, but may also be found occupying sites where a shallow, rocky soil overlies a deep heavy clay which is the B horizon of a buried soil (Van Dijk 1959). Frequently, but by no means invariably, it occupies sites of somewhat higher elevation than the neighboring *E. melliodora—E. blakelyi* Woodlands, but there is little or

[1] The system of classification of the vegetation is that proposed by Beadle and Costin (1952).

no evidence that any microclimatic differences in the habitats of these two communities are sufficient to justify the assumption that their distribution is climatically controlled. The fact that *E. rossii* is found both above and below *E. melliodora—E. blakelyi* certainly suggests that a climatic effect is unlikely. Field evidence indicates that one or more soil properties are more likely to be affecting the distribution of the Eucalypts.

The trees are of typical forest form, i.e. branching commences more than half way up the bole (cf. Beadle and Costin 1952). Tree height varies with the site, being from about 30-70 ft. (8-18 m.). The canopy is somewhat open, with tree crowns touching but not interlacing. The development of a shrub stratum varies with the site, and probably also with the frequency of fire. There may be a few scattered tall shrubs ($>$ 2 m.), and usually a rather poorly developed small shrub ($>$ 2 m.) stratum. The more prominent small shrubs include *Brachyloma daphnoides* (Sm.) Benth., *Stypandra glauca* R. Br., *Daviesia corymbosa* Sm., *Hibbertia linearis* R. Br., *Melichrus urceolatus* R. Br., and *Lissanthe strigosa* (Sm.) R. Br. and less frequently species of *Acacia, Pultenaea, Dillwynia, Hakea, Grevillea* and *Pimelea.* The herbaceous stratum consists of widely scattered grasses and forbs, growing frequently in pockets of deeper soil amongst rocks, where moisture supply and fertility may be somewhat augmented. In this stratum may be found species of *Danthonia* and *Stipa,* with *Poa caespitosa* in the wetter and colder parts of the range of this community, and a number of annual and perennial forbs. The herbaceous stratum is never well developed.

The *E. melliodora—E. blakelyi* Savannah Woodland occurs commonly on the Southern Tablelands and elsewhere in New South Wales and in Victoria, but is not found in areas where cold air drainage materially affects winter temperatures. The trees vary in height from about 40-70 ft (10-18 m.), have a typical woodland form with branching less than half-way up the bole, and a spreading crown (cf. Beadle and Costin 1952), and are so spaced that the distance between crowns is approximately equal to the diameter of the crown. On particularly favourable sites a Tall Woodland Form (Beadle and Costin 1952) may develop.

The E. melliodora—E. blakelyi Association occurs on deeper and more mature soils than does the *E. rossii* Association, these soils being commonly influenced by colluvial material brought from higher levels. Topography may be from virtually flat to gently undulating, and the community is seldom found on steep slopes. Because of the open nature of the community and the favorable soils, a well developed herbaceous stratum is present, dominated by perennial grasses, which in the undisturbed condition were chiefly *Themeda australis* and *Poa caespitosa* with some of the tall *Stipa aristiglumis sens. lat.* With disturbance following settlement, these tall caespitose grasses have been largely eliminated and their place taken by various species of *Stipa* and *Danthonia* (cf. Moore 1953). Shrubs are rare in this community.

At the lower elevations the *E. pauciflora—E. rubida* Association is found where accumulation of cold air from surrounding hills causes frost pockets. It may be separated from the *E. rossii* Association by a belt of *E. melliodora—E. blakelyi* Woodland, and if sufficiently low temperatures are reached, there may be an area of grassland in the lowest part of the frost pocket. The community is structually similar to that at the higher elevations, with an herbaceous stratum dominated by perennial grasses. In the original conditions these grasses were chiefly *Poa caespitosa* and *Themeda australis,* but with disturbance following settlement these have to a large extent been replaced by *Danthonia* spp. A few small shrubs may be present, but are not a prominent feature of the community.

The *E. pauciflora—E. rubida* Association at higher altitudes is found on the low hills surrounding the frost pockets where the *Poa caespitosa* Grassland develops. This community is similar to that described above for the frost pockets of the lower elevations, with a well developed herbaceous stratum of perennial grasses, chiefly *Poa caespitosa,* but there may also be some development of chamaephytic shrubs. These sub-alpine communities are considerably influenced by the occurrence of snow during the winter, and by strong cold winds. Snow usually persists for two to three months, and at no time of the year is this area free from killing frosts.

The *Poa caespitosa* Association is a sub-alpine grassland found only in cold habitats, especially in frost pockets at relatively high altitudes (4,000 to 5,000 ft), and it is therefore much more restricted in range than the other three communities. It is similar in many respects to the Alpine Herbfields which may be found above the limit of tree growth at altitudes of more than 6,000 ft. The dominant species in the grasslands is *Poa caespitosa,* and in general other species present are of relatively minor importance. Associated species

include annual and perennial forbs. Shrubs are absent.

The *E. melliodora—E. blakelyi* Association commonly occurs adjoining the *E. rossii* Association, with a sharp boundary separating the two communities. Five such sites (1-5) were chosen and the soils of the two communities compared. Similarly, the *E. rossii* and the *E. pauciflora—E. rubida* Associations frequently occur as adjoining communities, and again five sites (6-10) were selected and the soils compared. At the higher elevations, the *Poa caespitosa* Association commonly adjoins the *E. pauciflora—E. rubida* Association, with a particularly sharp boundary between the two communities. Again, a comparison of the soils from five sites (11-15) was made.

The soils at Sites 1-10 are usually regarded as podzolics (Stephens 1950; Prescott 1952; Costin 1954), but Downes (1954) has suggested that they might better be regarded as solodic soils developed under the influence of cyclic salt. More recently Van Dijk (1959) has shown that in the Southern Tablelands Region there have been a number of cycles of soil formation and soil erosion, so that on many sites one or more buried soils may be found. Further, the soil currently appearing at the surface may have been formed during the most recent period of deposition and soil formation, or it may be one of the older soils which has escaped complete erosion or burial during periods of erosion and deposition after its formation. The soil parent materials at Sites 1-10 are chiefly Ordovician and Silurian sediments, including sandstones, quartzites and shales. At Site 5 the parent material is a basic igneous intrusion, while at Site 9, it is granite. The occurrence of *E. rossii* on soils derived from igneous rocks is unusual, especially on basic igneous rock such as is found at Site 5.

At the higher elevations (Sites 11-15) both the woodlands and grasslands occur on a range of soils (Costin 1954) derived from a wide range of parent material. At the sites sampled for this study, the soil parent materials were limestone, shale, volcanic tuff, granite and basalt.

Methods

Soils were obtained from four locations within each of the five neighbouring stands selected for each comparison, sampling being to a depth of 4 inches (10 cm.) or more, depending on the depth of the A horizon. The soils were sieved to remove stones and plant roots, and the four samples of each stand thoroughly mixed before being placed in pots in the glass house. Laboratory determinations were made on samples obtained after this mixing. Algerian oats (*Avena byzantina* C. Koch) were used to determine the nutrient status of the soils in respect of the major elements (Ca, N, P, K and S) and copper, manganese and zinc. To determine the molybdenum status, and at the same time to provide additional information regarding the calcium status, *Trifolium subterraneum L.* (subterranean clover, Mt. Barker strain) was used as the test plant.

The oats were grown in plastic pots containing from 700-900 gm. of air dry soil. In the major element trial, 9 plants were established in each pot, and the oats harvested 5 weeks (Sites 1-5) or 6 weeks (Sites 6-15) after sowing pregerminated seed. In the minor element trial, 4 plants were established in each pot, and harvested 151 days after sowing.

The subterranean clover was grown in enamel pots of 4½ in. (11.5 cm.) diameter containing 1000-1500 gm. air dry soil, with four plants per pot. As the pH of the soils from the *E. rossii* communities was generally below 5.5, a lime treatment was included, as Anderson and Moye (1952) have shown that applications of molybdenum are

Table I. Nutrients applied to soils in pot culture experiments, and rates of application

Algerian Oats

1. CaNPKS	7. NIL	
2. NPKS	8. Cu Mn Zn	+ NPKS
3. NPK	9. Cu Zn	+ NPKS
4. NPS	10. Cu Mn	+ NPKS
5. NKS	11. Mn Zn	+ NPKS
6. PKS	12. NIL	+ NPKS

Rates of Application per acre

Ca ≡ 1 ton Ca $(OH)_2$

N ≡ 2 cwt. $(NH_4)_2 SO_4$

P ≡ 4 cwt. superphosphate (22% P_2O_5)

K & S ≡ 1 cwt. $K_2 SO_4$

Cu ≡ 7 lb. Cu $SO_4.5H_2O$

Zn ≡ 7 lb. Zn $SO_4.7H_2O$

Mn ≡ 14 lb. Mn $SO_4.7H_2O$

Subterranean Clover

1. PKS
2. PKS + Mo
3. PKS + Ca $(OH)_2$
4. PKS + Mo + Ca $(OH)_2$

Rates of Application

PKS as for Algerian Oats

Mo ≡ 20 oz/ac. sodium molybdate

$Ca(OH)_2$ ≡ 2cwt/ac.

not effective at low pH. The seed was inoculated with *Rhizobium* culture, and the plants harvested just prior to flowering.

Details of the treatments applied and the rates of application of nutrients are shown in Table I. The pots were weighed at regular intervals and water added to maintain the soil moisture as near as practicable at the moisture equivalent.

Moisture equivalent, soil pH on a 1 : 5 suspension in water, and total nitrogen by Kjeldahl digestion using selenium as a catalyst, were determined according to Piper (1942). Available phosphorus in the soils was determined by the method of Williams (1950).

Exchangeable metal cations were determined by leaching with normal ammonium chloride (Piper 1942). Sodium, potassium and calcium were determined directly on the ammonium chloride leachate using an "E.E.L." flame photometer. Magnesium was determined directly on the leachates by atomic absorption spectroscopic analysis (David 1958).

Exchangeable hydrogen was determined at pH 7.0 by the *p*-nitrophenol buffer method of Schofield (1953), by extrapolation to pH 7.0 as suggested by Piper (1936). Cation exchange capacity at pH 7.0 was obtained as the sum of the exchangeable metal cations and exchangeable hydrogen.

All determinations were made on air-dry soil.

Plant phosphorus was determined by the molybdovanadate method of Cavell (1955) modified to follow a nitric-perchloric-sulphuric acid digestion of the plant material.

Results

Details of the results of the trials with copper, manganese and zinc are not reported. In most soils no response to these elements was obtained. There was some indication of a difference in the zinc status of the soils of the *E. rossii* and *E. melliodora* communities (Sites 1-5) but further work is necessary to confirm this.

Table II shows the mean response of oats to the major elements (Ca, N, P, K, S). Significant differences between communities have been demonstrated for the phosphorus, nitrogen and potassium status of the soils.

Table III shows the mean yield of oats for each treatment, together with the significance of the response to each element within communities. All soils are deficient in phosphorus and nitrogen, whilst deficiencies of potassium, sulphur or calcium appear to be associated with some communities.

The response of subterranean clover to molybdenum and lime is shown in Table IV. No significant differences between communities in response to molybdenum were obtained in the absence of lime. At Sites 1-5 and 6-10 there was a significant difference between communities in their response to lime.

In Table V, mean yields of subterranean clover are given for each treatment, together with the significance of the responses within communities to molybdenum and lime. In only one soil (subalpine grassland) is a response to molybdenum alone obtained, while all soils show a significant response to lime.

The mean values for soil pH, total nitrogen and available phosphorus, together with the range of values for moisture equivalent, are shown in Table VI. There are no significant differences in soil nitrogen or available phosphorus but significant

Table II. Mean response of oats to major elements. (g dry matter/pot)

Sites	Response to									
	Ca		N		P		K		S	
	Er	Em	Er	Em	Er	Em	Er	Em	Er	Em
1- 5	0.331	0.016	0.759	1.075	0.619	1.084	0.091	0.231	0.336	0.499
	N.S.		P<.01		P<.01		P<.05		N.S.	
	Er	Ep	Er	Ep	Er	Ep	Er	Ep	Er	Ep
6-10	0.220	−0.123	0.875	1.428	0.838	1.413	0.292	0.488	0.183	0.427
	N.S.		P<.05		P<.01		N.S.		N.S.	
	Ep	G	Ep	G	Ep	G	Ep	G	Ep	G
11-15	0.113	0.059	0.701	1.084	1.478	1.654	0.208	0.340	0.298	0.424
	N.S.		P<.05		N.S.		N.S.		N.S.	

Er=E. rossii D.S.F.; Em=E. melliodora-E. blakelyi S.W.; Ep=E. pauciflora-E. rubida S.W.; G=Poa caespitosa Grassland

TABLE III. Mean yield of Oats (g. dry matter/pot)

Sites	Community	Treatment						
		CaNPKS	NPKS	NPK	NPS	NKS	PKS	NIL
1- 5	E. rossii D.S.F.	1.358	1.027	0.691	0.936	0.408	0.268	0.335
	E. melliodora-E blakelyi S.W.	1.670	1.654	1.155	1.423	0.570	0.579	0.673
6-10	E. rossii D.S.F.	1.562	1.342	1.159	1.050	0.504	0.467	0.369
	E. pauciflora-E rubida S.W.	1.807	1.930	1.503	1.442	0.517	0.502	0.450
11-15	E. pauciflora-E. rubida S.W.	2.838	2.725	2.427	2.517	1.247	2.024	1.040
	Poa caespitosa Grassland	2.530	2.471	2.047	2.131	0.817	1.387	0.776

Sites	Community	Significance of Response to				
		Ca	N	P	K	S
1 -5	E. rossii D.S.F.	P<.01	P<.001	P<.001	N.S.	P<.01
	E. melliodora-E. blakelyi S.W.	N.S.	P<.001	P<.001	N.S.	P<.01
6-10	E. rossii D.S.F.	N.S.*	P<.001	P<.001	P<.05	N.S.
	E. pauciflora-E. rubida S.W.	N.S.	P<.001	P<.001	P<.001	P<.001
11-15	E. pauciflora-E. rubida S.W.	N.S.	P<.01	P<.001	N.S.	N.S.
	Poa caespitosa Grassland	N.S.	P<.001	P<.001	P<.05	P<.01

* Least difference for significance at 5% = 0.226

TABLE IV. Mean response of subterranean clover to molybdenum and lime (g. dry matter/pot)

Sites	Response to									
	Mo		$Ca(OH)_2$		Mo + $Ca(OH)_2$		Mo in presence of $Ca(OH)_2$		$Ca(OH)_2$ in presence of Mo	
	Er	Em	Er	Em	Er	Em	Er	Em	Er	Em
1- 5	0.86	1.16	6.94	1.70	9.59	1.60	2.65	−0.09	8.73	0.44
	N.S.		P<.01		P<.01		P<.01		P<.01	
	Er	Ep	Er	Ep	Er	Ep	Er	Ep	Er	Ep
6-10	−0.19	2.15	9.25	5.41	10.14	6.09	0.89	0.69	10.33	3.95
	N.S.		P<.05		N.S.		N.S.		P<.05	
	Ep	G	Ep	G	Ep	G	Ep	G	Ep	G
11-15	1.21	1.58	3.21	3.63	3.53	4.34	0.32	0.71	2.32	2.76
	N.S.		N.S.		N.S.		N.S.		N.S.	

Er = E. rossii D.S.F.; Em = E. melliodora-E. blakelyi S.W.; Ep = E. pauciflora-E. rubida S.W.; G = Poa caespitosa Grassland.

TABLE V. Mean yield of subterranean clover (g. dry matter/pot)

Sites	Community	Treatment				Significance of Response to				
		NIL (1)	Mo (2)	$Ca(OH)_2$ (3)	Mo + $Ca(OH)_2$ (4)	Mo (2)−(1)	$Ca(OH)_2$ (3)−(1)	Mo + $Ca(OH)_2$ (4)−(1)	Mo in presence of $Ca(OH)_2$ (4)−(3)	$Ca(OH)_2$ in presence of Mo (4)−(2)
1- 5	E. rossii D.S.F.	2.76	3.62	9.71	12.35	N.S.	P<.01	P<.001	N.S.*	P<.01
	E. melliodora-E. blakelyi S.W.	15.12	16.28	16.81	16.72	N.S.	P<.05	P<.05	N.S.	N.S.
6-10	E. rossii D.S.F.	4.07	3.88	13.32	14.21	N.S.	P<.01	P<.001	N.S.	P<.01
	E. pauciflora-E. rubida S.W.	10.55	12.70	15.95	16.65	N.S.	P<.05	P<.01	P<.05	P<.01
11-15	E. pauciflora-E. rubida S.W.	12.41	13.61	15.61	15.93	N.S.	P<.05	P<.05	N.S.	N.S.
	Poa caespitosa Grassland	10.63	12.21	14.26	14.97	P<.05	P<.001	P<.001	N.S.	P<.01

* Least difference for significance at 5% = 2.71

TABLE VI. Mean values for pH, total nitrogen and available phosphorus, and range of values for moisture equivalent of the soils

	SITES 1-5		SITES 6-10		SITES 11-15	
	E. rossii D.S.F.	E. melliodora -E. blakelyi S.W.	E. rossii D.S.F.	E. pauciflora -E. rubida S.W.	E. pauciflora -E. rubida S.W.	Poa caespitosa Grassland
pH	4.78	5.79	5.36	6.27	6.13	5.97
	P<.01		P<.01		N.S.	
Total N (%)	0.11	0.12	0.09	0.06	0.25	0.24
	N.S.		N.S.		N.S.	
Available phosphorus (p.p.m. PO_4)	64.9	89.8	84.0	50.2	364.2	408.7
	N.S.		N.S.		N.S.	
Moisture Equivalent (%)	18.9-23.4	15.8-22.3	13.6-29.2	12.5-20.2	33.9-41.8	29.4-40.4

differences between communities are shown for soil pH for sites 1-5 and 6-10.

The data in Table II indicate differences in the available phosphorus status of the soils of the forest and woodland communities at Sites 1-5 and 6-10, but this has not been confirmed by the soil analyses. Many procedures for the extraction and estimation of "available" soil phosphorus have been suggested, and it is possible that the results obtained based on the response of oats might be confirmed by using a different method of soil analysis. The choice of Williams' (1950) method was made because in developing it he was able to correlate plant growth with a particular fraction of the soil phosphorus which he suggested as an index of the "available" phosphorus. It would be anticipated that differences in the phosphorus status of the soils would be reflected in the phosphorus content of the plant material, expressed either as relative or absolute phosphorus content. Table VII shows the phosporus content of the oats grown on the nil and NKS treatments, but for the soils of Sites 1-5 and Sites 6-10 there are no significant community differences. A difference in phosphorus uptake was found between the two subalpine communities (Sites 11-15).

The marked response of subterranean clover to lime, together with the low pH of the soils of the *E. rossii* communities, suggested that an examination of the exchangeable cations in the soils would assist in the interpretation of the results. Table VIII shows the mean values for exchangeable cations, together with total exchange capacity and percent hydrogen saturation. The soils of the *E. rossii* communities have lower exchangeable calcium, higher exchangeable hydrogen, and higher percentage hydrogen saturation than do those of the neighbouring *E. melliodora* and *E. pauciflora* woodlands. This applies particularly to the soils developed on sedimentary rocks, in which the exchangeable calcium of the soils of the *E. rossii* communities at Sites 1, 2, 3 and 4 varies from nil to 0.4 me. percent, with a mean value of 0.15 me. percent, and at Sites 6, 7, 8 and 10 from nil to 0.5

TABLE VII. Mean relative and absolute phosphorus content of oats from NIL and NKS treatments

Sites	Community	NIL TREATMENT		NKS TREATMENT	
		Relative P content (%P)	Absolute P content (mg.P)	Relative P content (%P)	Absolute P content (mg.P)
1-5	E. rossii D.S.F.	.365 } N.S.	1.5 } N.S.	.084 } N.S.	.345 } N.S.
	E. melliodora-E. blakelyi S.W.	.552 }	3.0 }	.109 }	.688 }
6-10	E. rossii D.S.F.	.655 } N.S.	2.2 } N.S.	.061 } N.S.	.320 } N.S.
	E. pauciflora-E. rubida S.W.	.639 }	2.9 }	.058 }	.298 }
11-15	E. pauciflora-E. rubida S.W.	.998 } N.S.	10.9 } P<.05	.089 } P<.05	1.179 } P<.05
	Poa caespitosa Grassland	.804 }	6.4 }	.069 }	.588 }

TABLE VIII. Mean values for exchangeable cations (me%) and % hydrogen saturation of the soils

Cation	Sites 1-5			Sites 6-10			Sites 11-15		
	E. rossii	E. melliodora	Sig. of Diff. between communities	E. rossii	E. pauciflora	Sig. of Diff. between communities	E. pauciflora	Poa caespitosa	Sig. of Diff between communities
Potassium	.35	.56	N.S.	.25	.20	N.S.	1.02	.89	N.S.
Sodium	.05	.03	N.S.	.08	.08	N.S.	.07	.05	N.S.
Calcium	1.00	5.56	P<.01	.64	1.84	P<.05	6.34	4.18	N.S.
Magnesium	1.6	1.8	N.S.	.94	.73	N.S.	1.7	1.5	N.S.
Hydrogen	11.99	4.18	P<.01	9.65	2.65	N.S.*	13.41	13.14	N.S.
Total Exchange capacity	14.99	12.13	N.S.	11.56	5.50	N.S.	22.55	19.77	P<.05
% H. saturation	80.02	37.83	P<.01	81.27	48.01	P<.01	59.20	64.46	N.S.

* F=6.55. For significance at 5% level, F=7.71. See Text and Table 9.

me. percent, with a mean value of 0.18 me. percent.

Although an analysis of the data for exchangeable hydrogen for Sites 6-10 failed to show a significant difference between the soils of the two communities at the 5 percent level, there seems little doubt that there is a real difference between them. Table IX shows the individual values for exchangeable hydrogen at each Site. It is clear that the value for the *E. rossii* soils is always greater than that for the corresponding *E. pauciflora* soils, while the highest value for *E. pauciflora* soils does not equal the lowest for the *E. rossii* soils. It would seem that the very high value for the *E. rossii* soil at Site 7 (20.33 me. percent) increases the variance to such an extent that a significant difference cannot be demonstrated. The fact that there is a difference in the percentage hydrogen saturation between these two groups of soils lends support to the conclusion that the soils differ in exchangable hydrogen.

TABLE IX. Exchangeable hydrogen (me%) in soils of Sites 6-10

Site	Community	
	E. rossii	E. pauciflora
6	8.48	4.20
7	20.33	2.60
8	7.97	2.80
9	4.30	1.95
10	7.18	1.70
Mean	9.65	2.65

Table X presents data for exchangeable calcium at Sites 5 and 9.

DISCUSSION

It is evident from the result reported above that nutrient deficiencies, as determined by the response of oats and subterranean clover to added nutrients, are associated with the soils of the communities studied. Responses to both nitrogen and phosphorus were obtained for all soils, while deficiencies of calcium, potassium, sulphur and molybdenum also occur. (See Tables III and V.) It is also seen that the communities are associated with soils in which the availability of nutrients to oats or subterranean clover may differ (Tables II and IV). Significant differences have been shown in nitrogen, phosphorus and potassium status, as determined by the response of oats, and in calcium and molybdenum status as determined by the response of subterranean clover.

TABLE X. Exchangeable calcium (me%) in soils of Sites 5 and 9, and mean values for the remaining Sites

	E. rossii	*E. melliodora*
Site 5	4.40	10.40
Mean for Sites 1-4	0.15	4.35
	E. rossii	*E. pauciflora*
Site 9	2.50	2.50
Mean for Sites 6, 7, 8 & 10	0.18	1.68

The result obtained in the comparison of the *E. pauciflora—E. rubida* Woodland and the *Poa caespitosa* Grassland Associations of the sub-alpine regions do not suggest any soil factor associated with the delimitation of these two communities. It is considered that the differences in soil nitrogen result from the different kinds of vegetation. The negative evidence obtained in this study indirectly supports the conclusions reached by Moore (1956) regarding the importance of temperature in this region.

The evidence for an edaphic factor or factors governing the distribution of the woodland and forest communities examined is much more favorable, but it is again likely that the differences

in soil nitrogen are the result of the different kinds of vegetation.

The response of oats to added phosphorus on the different soils indicates that there is a correlation between soil phosphorus and plant community. This has not been confirmed by chemical analysis of either the soils or the plants (Tables VI and VII), and this lack of confirmation, together with the low level of phosphorus in the soils of all four communities studied, suggests that soil phosphorus is not likely to be a major factor in the delimitation of the communities. However, the data obtained so far cannot be regarded as conclusive. The effects of varying levels of soil phosphorus on the native plants must first be determined before final conclusions can be drawn.

Beadle (1954) has shown that the most xeromorphic communities in the Sydney district (e.g. those occurring on Hawkesbury sandstone) occur on the soils with the lowest available phosphorus, whereas the most mesic (e.g. the Wet Sclerophyll Forest and Rain Forest) occur on the soils of highest available phosphorus. He suggests that xeromorphism is related to phosphorus supply, and not water. It is of interest in this connection to note that of the communities studied in the present work, the more xeromorphic (i.e. the Dry Sclerophyll Forest) occurs on the soils in which there is the greatest amount of available phosphorus, as measured by the response of oats to added phosphorus. Hannon (1956) made a detailed study of the nitrogen status of the soils and plants of the Hawkesbury Sandstones, and points out that the soils are of low fertility, with phosphorus and nitrogen as the chief limiting nutrients. She states that "the level of available nitrogen is extremely low." The xeromorphism noted by Beadle (1954) might therefore be the result of general low nutrient supply, and in particular the combined low levels of both phosphorus and nitrogen, rather than to the low level of phosphorus alone. (Cf. the "bog xeromorphism" of Schimper 1903, and the "Standortslehre" of Walter 1950.)

An examination of the data for subterranean clover responses Tables IV and V) shows that for all soils there is a significant response to lime, and further that there are significant differences between the soils of the Dry Sclerophyll Forest and Woodland communities in respect of this element. On the *E. rossii* soils developed on sedimentary rock, the subterranean clover grown in the absence of lime showed symptoms of calcium deficiency (Millikan 1953).

Where *E. rossii* occurs on soils derived from igneous rocks (Sites 5 and 9) the level of exchangeable calcium is higher than that for the soils developed on the sedimentary rocks (Table X) and subterranean clover does not show symptoms of calcium deficiency although clear responses to lime at 2 cwt./ac. were obtained. The exchangeable calcium in the soils may be higher than that in some of the Woodland soils on the sedimentary rocks. However, the soils of the adjoining Woodlands are also relatively high in exchangeable calcium. Calcium deficiencies in the Dry Sclerophyll Forest soils are also indicated by the response of oats to lime (Table III).

There is a similar difference between the soils in respect of pH, the soils of the Dry Sclerophyll Forests having a lower pH than those of the Woodlands (Table VI). The soils showing the greatest response to lime have the lowest pH.

There are marked differences between the soils of the Dry Sclerophyll Forest and Woodland communities in respect of exchangeable calcium and hydrogen, and in the percentage hydrogen saturation (Table VIII). It is clear that the soils of the *E. rossii* communities are more highly leached than are those of the neighbouring Woodlands, and the results for the soils of the *E. rossii* communities developed on sedimentary rocks indicate distinct calcium deficiency for cultivated plants.

From the evidence available at this stage, it might be argued that the delimitation of the communities studied is determined by the status of exchangeable calcium and hydrogen in the soil. However, as has been pointed out previously, it is unwise to draw specific conclusions on the basis of single correlations. Further work is necessary to determine the effect of different levels of calcium and hydrogen on the development of the species concerned, as well as to examine additional soil characteristics in relation to the vegetation. One must also consider the possibility that the differences observed in the exchangeable hydrogen and calcium in the soils are the result of differences in the vegetation.

The fact that an edaphic factor is operating has been demonstrated by growing *E. melliodora* and *E. rossii* in pot cultures on soils from both *E. rossii* and *E. melliodora* communities, the Eucalypts being grown in both pure and mixed stands (Moore 1959). The data suggest that the tolerance ranges for some unknown edaphic factor overlap, and that either species can develop on either soil. If both species colonize a soil simultaneously, competition between them operates to restrict each to its own soil.

An explanation of the occurrence of *E. rossii* on the soils derived from igneous rocks (Sites 5

and 9) can therefore be advanced. A comparison of the data for these soils with that for the soils developed on the sedimentary rocks would suggest that *E. rossii* should not occur on them but that they should be occupied by one or other of the Woodland communities. But if *E. rossii* propagules reached these areas first, invasion by either *E. melliodora* or *E. pauciflora* is prevented.

In the past, the occurrence of the *E. pauciflora—E. rubida* Woodland communities on the Table lands has been attributed to climatic factors, notably temperature (Pryor 1939, Costin 1954). It occurs either in "frost pockets" at altitudes of about 2000 ft. or as a subalpine Woodland at higher altitudes. In the comparison of *E. rossii* and *E. pauciflora* communities, the stands from which soil samples were obtained were of the former category. The evidence reported above suggests that an edaphic factor may be operative in the separation of the Woodland from the Dry Sclerophyll Forest, but that the climatic factor results in the replacement of the *E. melliodora—E. blakelyi* Association by the *E. pauciflora—E. rubida* Association. Field evidence in support of this suggestion may frequently be found by a gradation down the slope from *E. rossii* to *E. melliodora—E. blakelyi* to *E. pauciflora—E. rubida.*

Though there is no reason to doubt the statement that the vegetation provides a measure of the environment, only limited use can be made of this concept in the absence of a measure of the various environmental factors. Vegetation can be used as an indicator of similar environments, but measurements of the environmental factors are necessary to enable the use of vegetation as a measure of differences between environments. Jacks (1946) reviewed the literature dealing with attempts to use natural vegetation as an indicator of land quality, and it would seem that this has not been as successful as one might wish. There has been insufficient investigation of the relationships between vegetation and habitat factors (especially soil and topographic factors) to allow the general use of vegetation as an indicator of land quality. Whittaker (1954a) has critically examined the evidence for plant indication, both as individual species and as plant communities. He has concluded, *inter alia*, that "Few characteristics of plant populations or communities are so unrelated to environment as to be without possible indicator significance," and that "the best indicators are those characteristics of plants, on any level, which have the strongest correlations with environmental factors and permit highest probabilities in statements about environmental factors."

Field observations on the Southern Tablelands of New South Wales and elsewhere cannot fail to impress the observer with the fact that the different species of *Eucalyptus* are particularly sensitive to habitat conditions. Though climatic factors (particularly temperature) seem in a few instances to exert a controlling effect on distribution, it more frequently happens that some edaphic factor appears to be responsible. The nature of the soil differences involved can rarely be determined without precise experimental data, though it has long been the practice of the farming community to judge the quality of the land in large measure by the species of *Eucalyptus* occurring on it.

In the present study, the results obtained for the effect of lime on the growth of subterranean clover are of particular value in providing the kind of information required to allow better correlations to be made between the natural community and land use. It is clear from the data that with rare exceptions (as when *E. rossii* is found on soil derived from an igneous rock), attempts to grow subterranean clover where *E. rossii* was the natural dominant are unlikely to be successful in the absence of lime.

Summary

1. Soils were collected from a number of natural plant communities on the Southern Tablelands of New South Wales, and the nutrient status assessed by pot culture experiments in which Algerian oats and subterranean clover (Mt. Barker strain) were used as the test plants.

2. Responses to Ca, N, P, K and S were obtained on most soils, and significant differences between communities were demonstrated in respect of N, P, K and Ca.

3. Data on plant growth were supplemented by the determination of soil and plant phosphorus, soil nitrogen, pH and exchangeable cations.

4. There is no evidence that the nutrient status of the soils, as determined by the growth of oats and subterranean clover, influences the relative distribution of the two subalpine communities compared (*E. pauciflora—E. rubida* Woodland and *Poa caespitosa* grassland).

5. There is evidence that an edaphic factor operates in the delimination of the *E. rossii* Dry Sclerophyll Forest and the *E. melliodora* or *E. pauciflora* Woodlands, and that the calcium status of the soil may be a factor of some importance. Further work is required to confirm this.

6. The Dry Sclerophyll Forest communities usually occur on soils which are grossly deficient in calcium. Where *E. rossii* is the natural dominant, it is unlikely that pasture improvement by the use of subterranean clover will be successful in the absence of lime.

References

Allard, H. A. 1942. Lack of available phosphorus preventing normal succession on small areas on Bull Run Mountain in Virginia. Ecology **23**: 345-353.

Anderson, A. J. and Moye, D. V. 1952. Lime and molybdenum in clover development on acid soils. Aust. Jour. Agric. Res. **3**: 95-110.

Bach, R. 1950. Die Standorte jurassischer Buchenwaldgesellschaften mit besonder Berücksichtigung der Böden (Humuskarbonatböden und Rendzinen). Ber. schweiz. bot. Ges. **60**: 51-152.

Beadle, N. C. W. 1954. Soil phosphate and the delimitation of plant communities in Eastern Australia. Ecology **35**: 370-375.

———, **and Costin, A. B.** 1952. Ecological classification and nomenclature. Proc. Linn. Soc. N.S.W. **77**: 61-82.

Billings, W. D. 1950. Vegetation and plant growth as affected by chemically altered rocks in the Western Great Basin. Ecology **31**: 62-74.

———. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. **27**: 251-265.

Braun-Blanquet, J. 1951. "Pflanzensoziologie." 2nd ed. Springer: Vienna.

Cain, S. A. 1944. "Foundations of Plant Geography." Harper and Bros.: New York and London.

Cavell, A. J. 1955. Colorimetric determination of phosphorus in plant material. Jour. Sci. Food Agric. **6**: 479-480.

Clements, F. E. 1928. "Plant Succession and Indicators." Wilson: New York.

———. 1936. Nature and structure of the climax. Jour. Ecology **24**: 252-284.

Coaldrake, J. E. 1951. The climate, geology, soils and plant ecology of portion of the County of Buckingham (Ninety-Mile Plain) South Australia. Comm. Sci. Industr. Res. Org. Aust. Bull. No. **266**.

———, **and Haydock, K. P.** 1958. Soil phosphate and vegetal pattern in some natural communities of southeastern Queensland. Ecology **39**: 1-5.

Costin, A. B. 1954. A Study of the Ecosystems of the Monaro Region of New South Wales with Special Reference to Soil Erosion. Govt. Printer: Sydney.

Crocker, R. L. 1952. Soil genesis and the pedogenic factors. Quart. Rev. Biol. **27**: 139-168.

David, D. J. 1958. Determination of zinc and other elements in plants by atomic absorption spectroscopy. The Analyst **83**: 655-61.

Downes, R. G. 1954. Cyclic salt as a dominant factor in the genesis of soils in Southeastern Australia. Aust. Jour. Agric. Res. **5**: 448-464.

Du Rietz, G. E. 1932. Vegetationsforschung auf Soziationsanalytscher Grundlage. Handbuch der biologischen Arbeitsmethoden. Abt. XI, T. 5, pp. 293-480. Ed. by Emil Abderhalden. Urban and Schwarzenberg: Berlin.

Ellenberg, H. 1953. Physiologisches und ökologisches Verhalten derselben Pflanzenarten. Ber. deutsch bot. Gesell. **65**: 350-361.

———. 1958. Bodenreaktion (einschliesslich Kalkfrage). Handbuch der Pflanzenphysiologie Vol. **IV**: 638-708.

Gates, D. H., Stoddart, L. A. and Cook, C. W. 1956. Soil as a factor influencing plant distribution on salt deserts in Utah. Ecol. Monog. **26**: 155-175.

Gorham, E. 1955. Vegetation and the alignment of environmental fatcors. Ecology **36**: 514-515.

Hannon, Nola J. 1956. The status of nitrogen in the Hawkesbury Sandstone soils and their plant communities in the Sydney district. I. The significance and level of nitrogen. Proc. Linn. Soc. N.S.W. **81**: 119-143.

Jacks, G. V. 1946. Land classification and land use planning. Imp. Bur. Soil Sci. Tech. Comm. No. **43**, pp. 31-40.

Jenny, H. 1941. "Factors of Soil Formation." McGraw-Hill: New York.

Knapp, R. 1954. "Experimentalle Soziologie der höheren Pflanzen." Ulmer: Stuttgart.

Krause, W. 1958. Boden und Pflanzengesellschaften. Handbuch der Pflanzenphysiologie Vol. **IV**: 807-850.

Kruckeberg, A. R. 1951. Instraspecific variability in the response of certain native plant species to serpentine soil. Amer. Jour. Bot. **38**: 408-419.

———. 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. Ecology **35**: 267-274.

Kucera, C. L. and Martin, S. C. 1957. Vegetation and soil relationships in the Glade region of the Southwestern Missouri Ozarks. Ecology **38**: 285-291.

Major, J. 1951. A functional, factorial approach to plant ecology. Ecology **32**: 393-412.

McMillan, C. 1956. The edaphic restriction of *Cupressus* and *Pinus* in the coast ranges of central California. Ecol. Monog. **26**: 177-212.

Millikan, C. R. 1953. Nutritional disorders in subterranean clover. Dept. Agr. Vic. Tech. Bull. No. **11**.

Moor, M. 1952. Die Fagion—Gesellschaften im Schweizer Jura. "Grüne Sammlung" Heft **31**. Hans Hauber: Bern.

———. 1952. Die Fagion—Gesellschaften im Schweizer Jura. Beitr. Geobot. Landesaufn. Schweiz. **31**: 1-201.

Moore, C. W. E. 1953. The vegetation of the Southeastern Riverina, New South Wales. I. The Climax communities. Aust. Jour. Bot. **1**: 485-547.

———. 1959. Interaction of species and soils in relation to the distribution of Eucalypts. Ecology **40**: In press.

Moore, R. M. 1956. Natural phenomena and microclimate. Australia—Unesco Symposium on Arid Zone Climatology with Special Reference to Microclimatology. Canberra. Paper **20**.

Piper, C. S. 1936. Exchangeable hydrogen in soils. Jour. Counc. Sci. Industr. Res. Aust. **9**: 113-124.

———. 1942. "Soil and Plant Analysis." University of Adelaide: Adelaide.

Prescott, J. A. 1952. The soils of Australia in relation to vegetation and climate. Comm. Sci. Industr. Res. Org. Bull. No. **52**.

Pryor, L. D. 1939. The vegetation of the Australian Capital Territory. M.Sc. Thesis, University of Adelaide.

Schimper, A. F. W. 1903. "Plant Geography upon a Physiological Basis." English Ed. Trans. W. R. Fisher. Clarendon Press: Oxford.

Schofield, R. K. 1933. Rapid methods of examining soils. II. The use of *p*-nitrophenol for assessing lime status. Jour. Agric. Sci. **23**: 252-254.

Specht, R. L. and Rayson, P. 1957. Dark Island heath (Ninety-mile Plain, South Australia). I. Definition of the ecosystem. Aust. Jour. Bot. **5**: 52-85.

Stephens, C. G. 1950. A mapping system for the compilation of a soil map of Australia. A system based on the taxonomy of the Great Soil Groups. Jour. Aust. Inst. Agric. Sci. **16**: 10-14.

Tansley, A. G. 1920. The classification of vegetation and the concept of development. Jour. Ecol. **8**: 118-149.

———. 1935. The use and abuse of vegetational concepts and terms. Ecology **16**: 284-307.

———. 1939. British ecology during the past quarter-century: the plant community and the ecosystem. Jour. Ecol. **27**: 513-530.

Van Dijk, D. C. 1959. Soil features in relation to erosional history in the vicinity of Canberra. Comm. Sci. Industr. Res. Org. Australia Soil Pub. No. **13**.

Vlamis, J. 1949. Growth of lettuce and barley as influenced by degree of calcium saturation of the soil. Soil Sci. **67**: 453-466.

———, **and Jenny, H.** 1948. Calcium deficiency in serpentine soils as revealed by adsorbent technique. Science **107**: 549.

Walker, R. B. 1954. The ecology of serpentine soils. II. The factors affecting plant growth on serpentine soils. Ecology **35**: 259-266.

Walter, H. 1950. Einführung in die Phytologie. Vol. 3, Pt. 1. p. **187**.

Whittaker, R. H. 1953. A consideration of the climax theory; the climax as a population and pattern. Ecol. Monog. **23**: 41-78.

———. 1954. The ecology of serpentine soils. IV. The vegetational response to serpentine soils. Ecology **35**: 275-288.

———. 1954a. Plant populations and the basis of plant indication. Festsch. Aichinger **1**: 183-206.

Williams, C. H. 1950. Studies in soil phosphorus. I. A method for the partial fractionation of soil phosphorus. Jour. Agric. Sci. **40**: 233-242.

Young, V. A. 1934. Plant distribution as influenced by soil heterogeneity in Cranberry Lake region of the Adirondack Mountains. Ecology **15**: 154-196.

NATURAL REPLACEMENT OF CHESTNUT BY OTHER SPECIES IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK[1]

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In 1904 the chestnut blight, caused by the fungus *Endothia parasitica,* was discovered in New York City. It had been introduced to this country from Asia on Asiatic chestnuts several years earlier and by the time it was recognized as a potential hazard it was already established in southern New England and probably uncontrollable even at that early date (Anonymous 1954; Gravatt 1949). Wherever chestnut trees were killed by the blight, openings were created in the forest canopy (Fig. 1). The natural closure of 2569 of these openings by other species of trees in the Great Smoky Mountains National Park has been the subject of this study.

[1] Contribution from the Botanical Lab., The Univ. of Tenn., N. Ser. 197. The work outlined in this paper was suggested by Mr. Arthur Stupka, Park Naturalist of the Great Smoky Mountains National Park, who also gave material aid and access to all parts of the Park. A grant-in-aid from the Tennessee Academy of Science made possible an extension of the field work. The Southern Forest Experiment Station, contributed clerical services and technical advice in the preparation of the manuscript.

The chestnut (*Castanea dentata* (Marsh.) Borkh.) was once among the largest of our hardwood trees. It reached greatest size in the mountains of eastern Tennessee and western North Carolina (Sargent 1933) where a height of 120 feet and a stem diameter of 8 feet, 5 feet above the ground, was reached. Throughout most of its range, however, it attained an average height of 80 to 100 feet and a diameter of 2 to 4 feet (Pinchot 1907). It was found in nearly every state east of the Mississippi and in Canada, ranging from sea level in Massachusetts to elevations over 5,000 feet in Tennessee and North Carolina. Early floras list it as occuring in Florida and southern Alabama, reports which have not been confirmed by herbarium specimens.

The causal fungus is pathogenic on all species of American and European *Castanea,* although in varying degrees. The sticky conidiospores are carried for long distances by insects, birds, and animals (Heald and Studhalter 1914), while the ascospores may be blown by wind (Metcalf 1912).

FIG. 1. Death of chestnut trees created holes in the canopy and allowed much light to reach the ground.

Details of its spread, virulence, and maleffects have been widely published.

The spores of the fungus germinate on open wounds in the bark and the mycelium grows throughout the bark, cambium, and outer sapwood. It spreads concentrically in the tree, girdling the stem. On smooth bark that has been infected, sunken areas appear which are soon covered with orange, yellow, or reddish brown masses of conidia about the size of a pinhead. Leaves above the girdle soon wither and die, but many remain on the dead tree in winter. After the limbs or trunks die, small brownish clusters of ascospores may be produced (Metcalf 1912).

Chestnut trees infected by the blight fungus do not die suddenly. At first, a few small limbs die, followed by the death of more and larger limbs, until finally, the entire tree succumbs. This slow demise of the tree may take place over a period of 2 to 10 or more years. The higher the elevation in the Great Smokies, the slower the death of the chestnut and consequent release of associated trees. During this period, the crowns of co-dominants expand, the growth rate of the seedlings and saplings established prior to the blight (advance reproduction) increases, and new seedlings may become established.

As Aughanbaugh (1935) points out, closure of the canopy in the chestnut openings created by the slow death of the chestnut is decidedly different from closure of openings created by cutting. The slow death of the blight-killed chesnuts makes it possible for adjacent trees to adjust gradually to the new conditions and occupy much of the space left vacant.

LITERATURE

Several intensive studies of chestnut replacement have been made in other regions of the United States. Five of these, by Korstian and Stickel (1927a; 1927b); Aughanbaugh (1935), Keever (1953), and Nelson (1955) are particularly pertinent.

In southern New England Korstian and Stickel (1927a; 1927b) found nine or more taxa replacing chestnut. These were *Quercus prinus, Q. rubra, Q. alba, Acer rubrum, Fraxinus americana, Quercus coccinea, Q. velutina, Acer saccharum* and *Carya* spp. They noted a loss of *Betula lenta* in stands where chestnut was blight-killed. Also, *Acer saccharum* entered into the stand composition where it had previously been absent. This is the only record where sugar maple plays a significant role in the succession following chestnut. The major roles of *Quercus rubra* and *Q. prinus* in replacing chestnut were stressed.

Aughanbaugh (1935) studied 1618 chestnut openings in Pennsylvania. He found that of the reproduction established prior to the blight, 13 species attained an abundance of one percent or more. In order of decreasing abundance, these were: *Quercus prinus, Acer rubrum, Quercus coccinea, Nyssa sylvatica, Sassafras albidum, Robinia pseudoacacia, Quercus velutina, Q. alba, Q. rubra, Carya glabra, Betula lenta,* and *Pinus rigida.* It should be noted that hickory is far down the list. Aughanbaugh's studies also indicate a trend from an oak-chestnut association to an oak association-complex. He found no evidence that an oak-hickory association was in the making. He says that "Under natural forest conditions, the species replacing chestnut comprise those that formerly most closely associated with it." In practically every locality red maple and chestnut oak were the two leading replacement species.

Keever (1953) investigated stands containing chesnut in Macon County, North Carolina. This is near the southern limits of the former oak-chestnut association. The relatively greater abundance of hickory and the smaller number of species which comprise the overstory trees imply drier habitats than those of the Smokies. Fifteen dominant tree species were found in the Macon County study. These were tallied, in order of total density and

frequency of occurrence in the six stands studied. In order of density, they were *Quercus prinus, Q. rubra* var. *borealis, Carya glabra* (including *C. ovalis*), *Quercus alba, Acer rubrum, Betula lenta, Pinus strobus, Robinia pseudoacacia, Oxydendrum arboreum, Quercus coccinea, Liriodendron tulipifera, Halesia carolina, Nyssa sylvatica* and *Sassafras albidum*. This combination of species may be more representative of the oak-hickory association than of the oak association-complex which seems to be developing in other regions.

Nelson's (1955) studies of chestnut replacement in the Coweeta area of western North Carolina show that about 11 taxa are most important in replacing chestnut. These are *Carya* spp., *Liriodendron tulipifera, Quercus velutina, Q. prinus, Acer rubrum, Q. alba, Betula lenta, Quercus rubra, Robinia pseudoacacia, Quercus coccinea,* and *Aesculus octandra*. This study was carried out in a mountainous region with a generally southern exposure. The large proportion of hickories Nelson found exceeds that found by Keever (1953) and places it in the oak-hickory association which she recognizes. (It is of interest that Nelson found *Magnolia acuminata, Betula alleghaniensis,* and *Tsuga canadensis* invading some sites unoccupied by these species when chestnut was present, indicative of a current trend for cove forest types to expand.) Nelson concluded that "the trend to date indicates that chestnut is being replaced primarily by the advancement of species which were codominant with chestnut and secondarily by invasions and the advancement of subordinate species."

Other investigations of chestnut replacement (Richards 1917; Illick 1921; Spaeth 1920; Nicholas 1925), have generally been based on reconnaissance rather than actual sampling and treat only the commercially important species. Results of these studies are in general harmony with the more intensive quantitative studies.

It may be inferred from these earlier studies and the present one that the important taxa which characterized the former oak-chestnut forest association, through their consistency of concurrence and joint dominance, were *Castanea dentata, Quercus prinus, Q. rubra, Q. alba, Q. coccinea, Acer rubrum,* and *Carya* spp. Two other species, *Quercus velutina,* and *Betula lenta* were also abundant throughout most of the oak-chestnut forest region. The hickories were generally not abundant and there seems to be little justification for including them in naming the probable future regional replacement of the oak-chestnut association.

The Study Area

The study of chestnut replacement reported herein was carried out in the Great Smoky Mountains of eastern Tennessee and western North Carolina. Some of the peaks are among the highest in the eastern U. S., with Clingman's Dome culminating at an elevation of 6,643 feet (King and Stupka 1950). The terrain is steep, with mountain streams cascading and plunging down steep mountain valleys. The soils are thin, rocky, and often poorly developed.

Kendeigh (1942) described the principal study area, in a list of research areas in the National Parks, as follows:

> Great Smoky Mountains National Park. 8. Biotic Succession Area. Probably the largest stand of dead mature chestnut in the park, between Indian Camp Creek, Texas Creek, the Pinnacle Lead and the Park Line, approximately 3800 acres. Altitude approximately 2000-6300 feet. Comprises a complex of several vegetative cover types, conforming in a general way to varying altitudinal limits in drainage basins. Spruce on highest ridges, and oak-chestnut on lower ridges. Lower parts of drainages are chiefly cove hardwoods, with northern hardwoods predominating in upper positions of valleys and slopes. Includes several old burns with reproduction 1-20 years old, also some grassland, Yellow Pine Hardwoods, and heath balds. Also a limited amount of White Pine Hardwoods.

The forests of the Great Smokies are within the Oak-Chestnut Association, as mapped by Braun (1950), with the cove forests strongly related to her Mixed Mesophytic Association. While Braun could find no sharp boundary between the chestnut, chestnut-yellow poplar, and oak-chestnut communities of the mesic slopes and the highly mesophytic communities of the coves, she pointed out that the typical representatives of each situation are quite different. The gradual transitions between cove and slope stands are difficult to describe and account for many unusual species combinations. Generally, however, stand boundaries follow natural topographic features, with those on southern exposure more sharply defined than northern ones.

Whittaker (1956) described the vegetation of the Smokies in detail, and suggested that Braun's Mixed Mesophytic concept is somewhat less applicable there than in the Cumberland Mountain region. He believed that the expression embraces too broad and heterogeneous a group of species. These differences in opinion on the status of the highly mesophytic cove forests, and their transitional types to ridges and slopes indicate the complex nature of the forests of the Smokies.

The climate of the Smokies may be described as perhumid, falling into a rain forest classification (Thornthwaite 1931; Shanks 1954). Annual rainfall at the highest elevations is in excess of 80 inches and at the lowest elevations about 60 inches. The 5-year mean of July temperatures at the base of the mountains was 74° F, with temperatures above 5000 feet averaging 10-15° F cooler (Shanks 1954). Under these cool moist conditions, plant growth is luxuriant and many species reach their maximum recorded size in the Great Smoky Mountains.

Methods

Thirty-five stands were intensively studied using a species check list, and a data form. Each stand was given a a reference number, then the location, elevation, aspect, and percent slope were recorded. Humus type and soil type were listed. Following this, the height and distribution pattern of shrubs, herbs, and tree reproduction were entered. Tree-canopy height was measured with an Abney level and percent coverage was estimated.

The pre-blight forest type was determined from the remaining dominant and co-dominant trees, plus the chestnut trees indicated by stumps and snags. The forest type at the time of study was also recorded. Probable future types were projected on the basis of the composition and character of existing reproduction. Size of the stand was estimated and increment borings made to determine the approximate date of release. Any evidence concerning fire history, such as faces and scars, was noted.

Detailed data were systematically recorded for 387 openings. The condition of the dead chestnut and its diameter breast high (d.b.h.) were recorded. When the dead chestnut had been cut,[2] an attempt was made to determine its age by counting growth rings. The percent of the opening filled by other species, the height of the replacing species, and the stand position of these species were entered. Data on the species filling in the gap included distance from the dead chestnut, height, and d.b.h. Species composition, height, and covering in percent were recorded for the shrub layer. Qualitative data were taken for tree seedlings and the herbaceous layer. The predetermined categories simplified qualitative observations and a systematic examination of the stands and individual openings provided both quantitative and qualitative data.

A total of 2569 openings in 79 stands was studied. Data recorded for these openings included replacing species, elevation, slope, and aspect.

Chestnut trees were not distributed uniformly throughout the Great Smokies, but were highly concentrated in some places, and absent in others. In extending this study to locations outside the principal study area (between Indian Camp Creek and Texas Creek) those areas were chosen in which chestnut was most abundant, to provide the maximum amount of information for the time spent.

The usage in scientific names follows Little's (1953) Check List, except for *Carya ovalis,* which Little includes in *Carya glabra.* For shrubs, herbs, grasses and other plants not in this check list, Gray's Manual of Botany (Fernald 1950) was used.

Stand types were named according to the method used in the Society of American Foresters' (1954) classification. Each type was required to be "distinctive and easily separated from other types which most closely resemble it." Many of the stand types recognized in this study would be classed as "subtypes" of the listed S.A.F. forest types. The area covered by most stands was greater than 5 acres, which was regarded as large enough for complete expression in nearly any topographic situation. However, a few were between one and 5 acres in size and one ridgetop stand covered less than one acre.

Results

Stands

Fifty species of trees were found in the 35 stands containing chestnut (Table I). The mesic nature of these stands is indicated by the high degree of presence of *Tsuga, Liriodendron, Magnolia fraseri, Halesia, Betula lenta, Tilia, Quercus rubra* and *Acer saccharum.* Half of the 16 most characteristic associates of chestnut in these stands are mesophytes. This large array of associated species identifies chestnut as a member of the rich cove forests in the Appalachian-centered oak-chestnut forest region as well as a dominant of the oak-chestnut forests for which the region is named (Braun 1950).

The shrubs in stands with chestnut (Tables I and II) often formed a very important stratum. *Rhododendron maximum,* for example, was present in 60% of all stands that were studied. At one extreme, it was found as an understory to hemlock, chestnut, and hardwoods in very mesic habitats, sometimes reaching a height of 15 to 20 feet. At the other extreme it was found in pine-chestnut-heath types as an associate of the more abundant *Kalmia latifolia* (Fig. 2). *Kalmia* was

[2] Some of the dead chestnuts had been cut in the mid-1930's to reduce the wildfire hazard in the National Park.

TABLE I. Presence of tree species in 35 stands containing chestnut

Species	Number of Stands	Percent of Stands
Acer rubrum	30	86
Tsuga canadensis	29	83
Lirodendron tulipifera	24	69
Magnolia fraseri	23	66
Quercus prinus	20	57
Halesia carolina var. monticola	19	54
Acer pensylvanicum	18	51
Aralia spinosa	17	49
Betula lenta	17	49
Fraxinus americana	16	46
Cornus florida	15	43
Quercus rubra	15	43
Quercus velutina	15	43
Tilia heterophylla	15	43
Acer saccharum	13	37
Nyssa sylvatica	13	37
Oxydendrum arboreum	12	34
Sassafras albidum	10	29
Betula alleghaniensis	9	26
Robinia pseudoacacia	9	26
Aesculus octandra	8	23
Acer spicatum	7	20
Fagus grandifolia	7	20
Magnolia acuminata	7	20
Magnolia tripetala	7	20
Ilex opaca	6	17
Hamamelis virginiana	5	14
Carya tomentosa	5	14
Carya ovalis	4	11
Picea rubens	4	11
Prunus serotina	4	11
Amelanchier laevis	3	9
Carya glabra	3	9
Quercus coccinea	3	9
Pinus pungens	2	6
Pinus rigida	2	6
Prunus pensylvanica	2	6
Quercus alba	2	6
Quercus falcata	2	6
Celtis occidentalis	1	3
Carya ovata	1	3
Cladrastis lutea	1	3
Juglans cinerea	1	3
Juglans nigra	1	3
Carya cordiformis	1	3
Pinus strobus	1	3
Diospyros virginiana	1	3
Liquidambar styraciflua	1	3
Ostrya virginiana	1	3
Morus rubra	1	3

TABLE II. Presence of shrubs and small trees in 35 stands containing chestnut

Species	Number of Stands	Percent of Stands
Rhododendron maximum	21	60
Kalmia latifolia	16	46
Pyrularia pubera	15	43
Aralia spinosa	12	34
Cornus florida	12	34
Sassafras albidum	10	29
Vaccinium spp.	9	26
Calycanthus fertilis	8	23
Clethra acuminata	7	20
Hamamelis virginiana	7	20
Lindera benzoin	7	20
Rubus spp.	7	20
Euonymus americanus	6	17
Euonymus obovatus	6	17
Ilex montana	6	17
Viburnum acerifolium	5	14
Hydrangea arborescens	5	14
Rhododendron (Azalea) spp.	4	11
Cornus alternifolia	3	9
Rubus canadensis	3	9
Sambucus canadensis	3	9
Amelanchier arborea	2	6
Gaultheria procumbens	2	6
Itea virginica	2	6
Rhododendron calendulaceum	2	6
Campsis radicans	2	6
Viburnum alnifolium	2	6
Rhododendron catawbiense	1	3
Rhus copallina	1	3
Viburnum cassinoides	1	3

characteristic of dry southern exposures as a dense understory to *Pinus rigida* and scattered chestnuts. Here, no chestnut replacement occurred and a pitch pine-heath resulted. On dry ridgetops, chestnut replacement is even slower (Fig. 3).

Shrubs and trees which never reach dominant or co-dominant canopy status were grouped together because of their overlap in range of height and similar role in the structure of the stand. *Rhododendron,* never of tree form, was often larger than *Cornus florida* and *Aralia spinosa,* which are normally small trees in an inferior stratum.

While some shrubs may be quite large or extensive, others, such as *Epigaea repens* and *Gaultheria procumbens* are low and semi-procumbent. *Viburnum alnifolium* is a representative of the

FIG. 2. Chesnut and pitch pine often occupied identicalecological niches on dry southern exposures.

highest elevations, while *Rhus copallina* was found at lowest elevations.

The importance of such species as *Medeola virginiana, Mitchella repens* and *Goodyera pubescens* emphasizes the northern affinities of the flora (Table III). Even though most of the species characterize mesic habitats, a few indicate more xeric sites, e.g., *Coreopsis major* and *Aster linarifolius*. The death of the chestnut undoubtedly created favorable light and soil moisture conditions for some invading species of low herbs, and resulted in a slight increase in the xerophytic element.

FIG. 3. Chestnut is very slowly replaced by other species on dry ridgetops, where the seed source is inadequate.

Of the vines found in stands with chestnut, *Smilax rotundifolia* was most often present, with *Parthenocissus quinquefolia* second (Table IV). Determining the abundance of vines presented special difficulties. Per cent ground cover, number of stems per unit area, and the other usual methods of expressing abundance quantitatively were not applicable, and the vines were never so abundant as to merit special attention.

Ferns and fern allies in stands with chestnut included *Adiantum pedatum, Asplenium platyneuron, Athyrium thelypteroides, Botrychium dissectum, B. obliquum, B. virginianum, Dennstaedtia punctilobula, Dryopteris spinulosa* var. *intermedia, D. noveboracensis, Osmunda cinnamomea, Polypodium polypodioides, P. virginianum, Polystichum acrostichoides, Pteridium aquilinum var. latiusculum, Lycopodium lucidulum* and *L. obscurum*. Ferns were sometimes an important part of the ground cover, often being very abundant and luxuriant. *Dryopteris spinulosa* var. *in-*

TABLE III. Occurrence of herbaceous ground cover in 35 stands containing chestnut

Species	Number of Stands	Percent of Stands
Medeola virginiana	16	46
Mitchella repens	15	43
Solidago spp.	15	43
Galax aphylla	14	40
Dioscorea spp.	13	37
Goodyera pubescens	10	29
Desmodium spp.	9	26
Viola spp.	9	26
Trillium spp.	7	20
Actaea pachypoda	6	17
Pilea pumila	6	17
Arisaema atrorubens	5	14
Polygonatum biflorum	5	14
Smilacina racemosa	5	14
Tipularia discolor	5	14
Aster spp.	4	11
Epigaea repens	4	11
Galium spp.	4	11
Gaultheria procumbens	4	11
Geranium maculatum	4	11
Gerardia laevigata	4	11
Hepatica acutiloba	4	11
Oxalis montana	4	11
Tiarella cordifolia	4	11

Species in 10 percent or fewer stands included: *Aletris farinosa, Campanula divaricata, Cimicifuga racemosa, Conopholis americana, Clintonia* spp., *Coreopsis major, Cymophyllus fraseri, Disporum lanuginosum, Eupatorium rugosum, Habenaria fimbriata, Impatiens pallida, Monarda didyma, Panicum* spp., *Ranunculus recurvatus, Scutellaria* spp., *Streptopus* spp., *Uvularia perfoliata.*

termedia is one of the taxa most likely to be present. On very dry, well-drained slopes, all fern species are scarce.

Individual Openings

A total of 5046 individual replacement trees was found in the 2569 chestnut openings. This included 182 openings in which there was no evidence of replacement. Three species comprised 46 percent of the replacements: *Quercus prinus, Q. rubra,* and *Acer rubrum* (Table V). These are also three of the most abundant species in other parts of the former oak-chestnut forest region (Korstian and Stickel 1927a; Aughanbaugh 1935; Keever 1953; Nelson 1955).

TABLE IV. Occurrence of vines in 35 stands containing chestnut

Species	Number of Stands	Percent of Stands
Smilax rotundifolia	21	60
Parthonocissus quinquefolia	15	43
Rhus radicans	10	29
Vitis spp.	8	23
Smilax glauca	4	11
Aristolochia durior	7	20
Campsis radicans	2	6
Clematis sp.	1	3

TABLE V. Relative abundance of major tree species replacing chestnut based on 5046 individuals

Species	Number of Individuals	Abundance in Percent
Quercus prinus	859	17
Quercus rubra	828	16
Acer rubrum	678	13
Tsuga canadensis	287	6
Halesia carolina var. monticola	231	5
Oxydendrum arboreum	228	4
Robinia pseudoacacia	204	4
Quercus coccinea	192	4
Liriodendron tulipifera	181	4
Betula lenta	148	3
Quercus alba	116	2
Fagus grandifolia	99	2
Cornus florida	97	2
Pinus rigida	90	2
Quercus velutina	90	2
Pinus pungens	76	1
Nyssa sylvatica	74	1
Betula alleghaniensis	64	1
Acer saccharum	51	1
Carya glabra	49	1
Acer pensylvanicum	46	1
Pinus echinata	40	1
Sassafras albidum	33	1
All other species	285	6

Tsuga canadensis and *Halesia carolina* var. *monticola,* comprising eleven percent of the replacements, again strongly emphasize the mesic nature of the forest stands with chestnut found in the Great Smokies (Table 5). These two species and the low abundance of *Carya* spp. set these stands apart from those studied by Keever (1953) and reveal the wide ecological amplitude of chestnut.

Oaks comprised 41 percent of all replacements, with no other genus approaching this high degree of abundance. This is probably a fair representation of the normal degree of association in the oak-chestnut region.

Three species had the greatest degree of presence in chestnut openings and were also most abundant; *Quercus prinus, Q. rubra* and *Acer rubrum* (Table 6). The dominance of this trio is accentuated by the drop from *Acer rubrum* (22%), to *Tsuga* (9%). After this drop, the decrease in occurrence of replacement species is gradual and more readily understood. In less mesic habitats than those at the Smokies, species such as *Pinus pungens, Carya glabra, Quercus coccinea,* and *Sassafras albidum* would be much more important.

TABLE VI. Occurrence of major replacement species in chestnut openings based on 2569 openings

Species	Number of Openings	Percent of Openings
Quercus prinus	626	24
Quercus rubra	625	24
Acer rubrum	576	22
Tsuga canadensis	221	9
Oxydendrum arboreum	208	8
Halesia carolina var. monticola	191	7
Robinia pseudoacacia	185	7
Liriodendron tulipifera	161	6
Quercus coccinea	157	6
Betula lenta	126	5
Quercus alba	101	4
Cornus florida	92	4
Quercus velutina	82	3
Fagus grandifolia	73	3
Nyssa sylvatica	73	3
Pinus rigida	59	2
Betula alleghaniensis	58	2
Pinus pungens	54	2
Acer saccharum	48	2
Acer pensylvanicum	46	2
Carya glabra	43	2
Sassafras albidum	30	1
Pinus echinata	26	1
Tilia heterophylla	26	1

Response of Suppresed Trees to Release

Suppressed trees, which had grown in no case over ten feet from the bases of overtopping chestnuts, were bored to obtain increment cores for study. Annual rings dating from 1920 to the date of sampling were measured to the nearest 1/1000 inch with a micrometer and hand lens. The width of each annual ring was converted to percent of total growth, based on the years since 1920, for each tree. Annual percents for a series of trees were averaged to give data depicted in Figure 4. Cores not showing a definite increase in radial growth following chestnut death were not used. Hemlock, chestnut oak, and northern red oak, in that order, yielded the best data for dating the progress of the blight in the Great Smokies. These species also showed the most vigorous and consistent response to release.

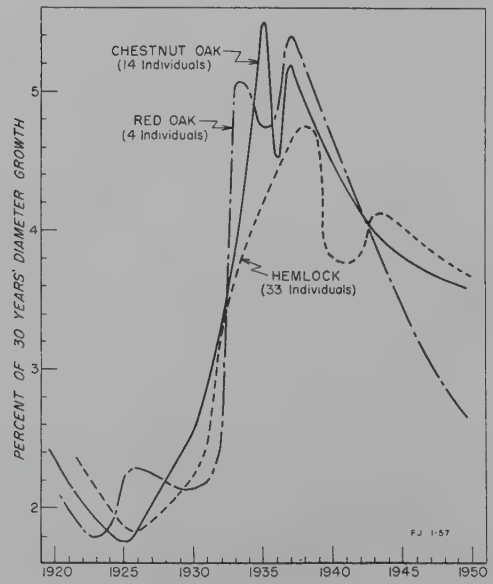

FIG. 4. Relative yearly diameter of 3 species of trees after release from chestnut competition.

Response of other species to release from chestnut dominance appears to have been generally a five stage procss:

(1) A 6 to 8 year period of slightly increased growth during which time crowns of co-dominants were probably filling out. Chestnuts were dying in this period.

(2) A 5 to 8 year period of greatly accelerated growth. This was apparently a response to the enlarged crowns.

(3) A 1 to 4 year period of rapid decrease in growth rate.

(4) A 2 to 4 year period of slightly accelerated growth.

(5) Beginning of a normal decline in growth rate as the released trees increased in size.

It appears that response to release from the chestnut began in 1925 or 1926. This is in general agreement with local and regional observations.

The sharp drop-off in growth immediately after or before the peak response years is not readily explained. It cannot be explained on a climatic basis because the three species dropped in different years. Possibly, the first major increase is the result of increased crown growth, while the secondary increase is due to the subsequent expansion of the root system.

All suppressed trees did not respond to release from suppression by chestnut by increasing in radial growth. Some species, such as *Halesia* and *Tilia* showed very little or no response to release. This was also true of *Rhododendron maximum*.

Variations With Site

Chestnut was found at elevations from below 2,000 feet to above 5,000 feet. All major replacement species were found below 3,000 feet, but above this elevation species dropped out at varying altitudes. *Cornus florida* was not found in association with chestnut at elevations over 3,500 feet. *Liriodendron* was not found higher than 4,000 feet and *Quercus velutina* not over 4,500 feet, while *Q. prinus* and *Tsuga* extended up to 5,000 feet.

Quercus rubra and *Fagus grandifolia* were the species in chestnut openings found most often above 5,000 feet. Both species are found in essentially pure stands on the top of ridges and in saddles at these elevations, with chestnut typically on the slopes around the edges. While beech and chestnut may often be associated at higher elevations, this is generally not true at lower elevations, where beech is found only in deeply shaded and consistently moist sites.

Chestnut is persisting at higher elevations with much greater tenacity than at low altitudes. At elevations above 4,500 feet many sprouting chestnut trees were found, often with fruits. It is possible that the fungus is either not as pathogenic in this cooler environment as it is on lower slopes or that a race of chestnut found at higher altitudes is less susceptible than the populations farther down the slope.

Aspect distribution of the 2569 openings was studied. It was found that the replacement species could be classified in three groups: (1) those primarily characteristic of a northerly exposure; (2) those mainly characteristic of a southerly exposure, and (3) those without a pronounced aspect correlation. Eastern and western exposures were not represented so often as others, and generally blended into either the northern or southern exposures, depending on such factors as slope and topographic position. *Quercus prinus, Q. rubra, Q. alba* were representative of species with no strong topographic affinity. Among the 15 species represented, *Quercus coccinea* was the only one on slopes with a pronounced southerly aspect. Among those characteristic of northern exposures were *Halesia, Liriodendron, Tsuga, Cornus florida* and *Fagus*.

Chestnut was found on a wide range of slopes, ranging from 0 to 90%. Grades of 40% were commonplace. The well aerated, rocky soil in which chestnut thrived is found on those slopes. *Quercus rubra, Betula lenta, Fagus,* and *Nyssa* were found with chestnut on very steep slopes more often than other species, particularly at high altitudes.

Discussion

Closure of Chestnut Openings

Chestnut openings were re-occupied by three basic processes, their relative roles determined by the dominant trees and character of the understory in the immediate vicinity of the blighted trees and the density of chestnut trees in the stand. These three processes may be summarized as follows:

(1) *Closure of the canopy by adjacent dominant and co-dominant trees in mature and over-mature stands.* This process has probably been most important in stands where chestnut crowns did not occupy more than 30-40% of the canopy and were sufficiently separate that openings were not contiguous. In these openings expansion of the crowns of co-dominants has been generally faster than increase in size of the advance reproduction. However, complete closure in some over-mature stands has not been completed even after 25 years because of slow response to environmental change, due to low growth potential of the over-mature trees.

(2) *Growth of advance reproduction.* Suppressed seedlings and saplings present at the time of the death of the chestnut reacted most rapidly to the increased amount of light. Both radial growth of stems and height growth were accelerated.

(3) *Growth of seedlings established subsequent to the death of the chestnut.* This method of replacement has been most important in stands where chestnut was the predominant species and where chestnut crowns were contiguous or overlapped. The greatly increased light at the soil surface permitted the survival of many seedlings which likely would have perished in the low light intensities typical of mature forests. Also, the reduced intensity of root competition for soil water may have been important even in the moist soils of the Smokies.

Pure or nearly pure stands of chestnut with a sparse herbaceous vegetation existed only on northern exposures. Stands on southern exposures with an equivalent density of chestnut were nearly always accompanied by a dense woody understory of *Kalmia, Rhododendron,* and *Vaccinium* in various mixtures.

Different replacement species responded differently to chestnut death. *Quercus prinus* and *Q. rubra,* the two most abundant species replacing chestnut, were often dominants or co-dominants at the time of death. Upon the development of the chestnut openings, the crowns of these species increased in size and closed the openings from the side.

Tsuga canadensis replaced chestnut by all three of the basic processes and often a dramatic increase in the evergreen component of the forest stands resulted. If we assume that hemlock is more mesic than chestnut, it may be inferred that death of the chestnut has, in such places, led to accelerated forest succession in a mesic direction. Chestnut and *Tsuga* had occurred together in stands as low as 3350 feet.

Robinia pseudoacacia probably increased in abundance proportionally more than any other species following death of chestnut. It entered the new openings rapidly and was most abundant in those where several chestnuts had died. The great increase in abundance of black locust was followed shortly by a major outbreak in locust leafminers. This caused a gradual weakening and decline of the black locust populations that was similar in slowness to the chestnut death. Secondary invasions by locust borers accelerated the decline of this species. As a result, black locust is rapidly resuming its subordinate place in the forests.

Acer rubrum is widely distributed throughout the forests of the Smokies at all altitudes. Seeds are shed in great abundance and germination percentage is usually high, so that young seedlings are numerous. However, mortality is great and usually only a very small fraction of these develop to maturity. When the chestnuts died, the openings in the canopy admitted more light than usual and a larger proportion of the seedlings survived. At the same time a larger proportion of the advance reproduction grew to maturity. *Liriodendron* and *Betula lenta* often responded in a manner similar to red maple by forming dense stands of saplings, especially in the very large openings. These stands are often found on very steep slopes.

Pinus rigida was often found growing with chestnut on dry southern exposures, usually with a dense understory of *Kalmia*. Upon death of the chestnut the heath became even more abundant. These were open stands, and there was no evidence that pine responded to release from chestnut.

Successional Trends Following Chestnut Death

Successional changes from the former oak-chestnut and cove forest types resulted from various combinations of the species replacements discussed in the foregoing section. As a basis for generalizations concerning present stages and predictions of probable future trends, 79 stands were studied in detail. To determine the "past type," the abundance of chestnut in stands prior to the blight was determined on the basis of dead trees, snags, stumps, and fallen trees still present. The "present type" was determined on the basis of trees present and alive at the time of the study. The "future type" was forecast on the basis of persistent canopy dominants, seedling reproduction, transgressives, and the relative tolerance of the various species to low light intensities. For example, it was inferred that understory hemlock seedlings and saplings included probable future canopy dominants because of the high shade tolerance of this species.

Prior to the blight, chestnut occurred in at least 27 distinct forest stand types in the Smokies. These included chestnut, red oak-chestnut, chestnut-pitch pine-heath, scarlet oak-chestnut, hemlock, hemlock-hardwoods, and mixed hardwoods.

At times, the loss of chestnut from forest stands seemed to accelerate successional changes already in progress, the death of the chestnuts giving impetus to make the shift very rapid rather than gradual. The most extreme example of this type of change was the shift from "pure" chestnut to hemlock, without an intermediate successional stage. This was made possible by the availability of hemlock seed from nearby hemlock stands. Some hemlock-hardwoods stand types, in which the hardwoods were largely chestnuts, also moved directly into a hemlock type. In other shifts from chestnut to hemlock, intermediate successional stages are apparent: hemlock-hardwood, red maple, and chestnut oak-red maple. Still other former oak-chestnut stands seem to be moving toward hemlock with a yellow-poplar intermediate stage. On other sites the yellow poplar does not seem likely to be replaced by another species within the foreseeable future. Mixed stands have sometimes shifted to a rather stable hemlock-hardwoods type.

The above examples all indicate the successional trend in the moister portion of the range of chestnut in the Great Smoky Mountains. Associated mesophytes were generally favored by the removal of chestnut dominance. The shift is most striking where hemlock is involved as a replacement, and a change from deciduous to evergreen forest is now in progress. However, in the intermediate and drier portion of chestnut habitat range, the residual stands, following death of chestnut, took several other courses.

In many cases, chestnut was replaced immediately by types which included red maple, apparently due to the abundant and widely dispersed seed supply of this species. However, there is no evidence from either these successional stands or stabilized old stands in the region that red maple will persist as a "climax" forest type.

Some stands changed composition only to the extent that chestnut was lost. These included mixed oak-chestnut, chestnut oak-chestnut, chestnut oak-chestnut-heath, chestnut oak-pitch pine-heath, red oak-chestnut-heath, and scarlet oak-chestnut. Chestnut in these stands was a co-dominant, and was less abundant than the accompanying dominants, so that changes were less

radical. The pitch pine-chestnut-heath combination reveals chestnut on perhaps its most xeric site—well drained, steep, rocky, slopes with a southern exposure. In these locations heath shrubs, mainly *Kalmia latifolia,* increased more than the pine after the chestnut death.

Studies of Blighted Stands

Many foresters have expressed concern as to the effects of losing chestnut from the forests of the eastern United States and several types of problems have been recognized. One of the major problems at the outset of the blight was devaluation of forest land (Ziegler 1920). The silvicultural problems, dealing with sustained management and chestnut replacement, have been explored (Retan 1918). Other writers have also explored various aspects of chestnut replacement (Barnes 1917; Toumey 1914; Perry 1922).

As early as 1924 Frothingham (1924) acknowledged the inevitable loss of chestnut in the southern Appalachians and proposed several types of studies designed to expedite management of blighted stands:

(1) Determination of rate and character of spread of the fungus. Gravatt and Marshall (1926) studied this aspect of the disease and made prognostications which turned out to be very good. They said that by 1935 nine-tenths of the counties in the southern United States would have reached the 80 percent infection stage. This was the case.

(2) Utilization of blighted trees. Studies such as those by Cruikshank *et al.* (1951) and Baxter and Gill (1931), on the utilization of dead chestnut for tannin production have been helpful in this respect.

(3) Studies of natural replacement. The works of Keever (1953), Nelson (1955), and Korstian and Stickel (1927a; 1927b) have yielded valuable information on this aspect of the problem.

(4) Studies of cultural replacement. In some regions, planting has been recommended (Richards 1914; Illick 1921). However, in spite of the vast areas of chestnut lost in the southern Appalachians, there has been very little planting. Now, since most of the gaps have been closed by natural processes, planting is not practical.

In retrospect, there have been very few and feeble attempts in the southern Appalachians to manage blighted stands from the standpoint of timber production. In the ten or fifteen years while chestnut death was acknowledged to be inevitable in the southern Appalachians, economic conditions were not such that a large quantity of the undiseased chestnut could be absorbed by the lumber and acid-wood market. After the blight, the stricken trees were too numerous to be used immediately, and they were soon degraded for lumber use by wood borers.

Recovery of the Chestnut

A number of writers found indications that the chestnut may develop an immunity or resistance to the blight (Collins 1920; Illick 1925; Hodson 1920; Wilber 1926). Aughanbaugh (1930) made an intensive study of this subject and concluded "it now appears possible that it [chestnut] may eventually recover its rightful position as one of our most important forest trees." However, in the same year Perry (1930) reported that chestnut sprouts infected with the blight failed to develop into trees. Recurring reports from local areas in the southern Appalachians that chestnut is "coming back" have not been confirmed in any case. No optimistic reports have appeared in more recent studies. While root systems, with their short-lived crops of sprouts, may continue to live for many years, no healthy trees were seen during the course of the present study. The fact that some sprouts bear fruits, especially at higher altitudes, is no indication of acquired immunity. Today, it appears that the American chestnut is, indeed, a doomed species.

There can be no hope that, once all of the blighted trees are dead, the source of the fungus will be removed and American chestnut can be reintroduced. The fungus is parasitic or saprophytic on a number of other species of American trees, although never so virulent as on *Castanca dentata* (Anonymous 1954). Post oaks have been more seriously harmed than any species other than chestnut (Anonymous 1954). Also many varieties of Asiatic chestnuts have been introduced which are blight resistant but will harbor the fungus indefinitely.

Great efforts have been made in the United States to develop blight-resistant American-Asiatic hybrid chestnut trees which will make high quality timber and fill the ecological niche once occupied by American chestnut (Clapper 1944, 1950; Diller 1950; Graves 1949). Nut production has also been regarded as an important, although seldom a paramount, objective of the breeding program. Breeding work was begun by the U.S. Department of Agriculture in 1909. Even though many blight-resistant hybrids have been developed and show promise, none have approached the grandeur of the American parent. Another problem seems to lie in the poor frost hardiness of the hybrids. The Asiatic chestnut is readily winter-killed, a characteristic usually transmitted genet-

ically. Breeding for disease is also being carried on in Europe, where the blight has attacked the indigenous species, *Castanea sativa* (Pavari 1949).

Nearly 50 years of empirical chestnut breeding work has not produced an acceptable hybrid for introduction as a forest tree. It is to be hoped that fundamental genetic work can be successfully carried out in the near future.

It should also be recognized that even if an acceptable hybrid were available, the time is past when chestnut can be re-established in our forests simply and easily. The openings have, for the most part, closed and drastic measures would undoubtedly be required to make stand conditions favorable for chestnut re-establishment.

Summary

(1) Chestnut (*Castanea dentata*) a major forest dominant in eastern United States, has been virtually eliminated since 1900 by the chestnut blight due to an introduced organism. It was a particularly important forest tree in the Southern Appalachians, when it began to die in the mid 1920's.

(2) The present study is concerned with the natural replacement of chestnut and consequent changes in forest composition in the Southern Appalachian region, based on primary data from 79 stands and 2569 individual openings created by the death of chestnut, in the Great Smoky Mountains of Tennessee and North Carolina.

(3) The most abundant species replacing chestnut were *Quercus prinus* (17%), *Quercus rubra* (16%), and *Acer rubrum* (13%). Species of *Quercus* comprised a total of 41% of the replacements.

(4) In the mesic cove stands there is often a tendency toward the development of more mesophytic forest types, generally including *Tsuga canadensis* as a replacement, and often *Liriodendron tulipfera, Magnolia fraseri, Halesia Carolina* var. *monticola, Tilia heterophylla* and *Acer saccharum*. On the dry slopes and ridges chestnut is being replaced by species more xerophytic than itself, such as *Oxydendrum arboreum, Quercus coccinea* and *Pinus rigida*.

(5) The death of chestnuts attacked by the blight was not sudden, but gradual. Occupation of the canopy and soil once filled by chestnut was usually begun by canopy expansion of co-dominants, growth of advance reproduction, or seedling growth even before the blighted trees were dead. Increment cores revealed that suppressed trees generally took nine to 15 years to reach maximum yearly growth increment following release. Increased annual growth began in approximately 1925-1926, indicating the arrival date of the fungus in the Great Smoky Mountains.

(6) No indication was found that the chestnut will "recover" or regain its former position as a dominant. Silvicultural practices in regions which once contained chestnut should be so predicated.

(7) The results of this study are in general agreement with those obtained in New England, Pennsylvania, and elsewhere in North Carolina. Of the unifying taxa of the former, broad oak-chestnut association, only *Carya* is of minor importance in the forests of the Great Smoky Mountains. The former oak-chestnut forest association is in process of developing into an oak association-complex, in which *Quercus prinus* and *Q. rubra* are likely to be particularly important.

References

Anonymous. 1954. Chestnut blight and resistant chestnuts. U.S.D.A. Farmers Bull. **2068**, 21 pp.

Aughanbaugh, J. E. 1930. Recovery of the chestnut in Pennsylvania. Pennsylvania Dept. of Forests and Waters Res. Cir. No. **1**, 17 pp.

———. 1935. Replacement of the chestnut in Pennsylvania. Pennsylvania Dept. of Forests and Waters Bull. **54**, 38 pp.

Barnes, L. C. 1917. Utilization and reforesting of chestnut-blighted lands. Jour. Forestry **15**: 854-858.

Baxter, D. V. and Gill, L. S. 1931. Deterioration of chestnut in the southern Appalachians. U.S.D.A. Tech. Bull. **257**, 21 pp.

Beattie, R. K. 1914. Bibliography of the chestnut tree blight fungus. Comm. for the Investigation and Control of the Chestnut Tree Blight Disease in Penn., 32 pp.

Braun, E. L. 1950. Deciduous Forests of Eastern North America. Philadelphia, 596 pp.

Clapper, R. B. 1944. American and blight-resistan chestnuts. The Flower Grower **31** (reprint, no pagi nation).

———. 1950. Breeding new chestnuts for southern forests. Forest Farmer **9**: 8.

Collins, J. F. 1920. Note on resistance of chestnut to the blight. Phytopath. **10**: 368-371.

Diller, J. D. 1950. The planting and care of blight-resistant chestnuts for forest trees. U.S.D.A. Forest Pathology Special Release **15**, 7 pp.

Fernald, M. L. 1950. Gray's Manual of Botany. Eighth Edition. New York, 1632 pp.

Frothingham, E. H. 1924. Some silvicultural aspects of the chestnut blight situation. Jour. Forestry **22**: 861-872.

Gravatt, G. F. 1949. Chestnut blight in Asia and North America. Unasylva **3**: 2-7.

——— **and Marshall, R. P.** 1926. Chestnut blight in the southern Appalachians. U.S.D.A. Cir. **370**. 11 pp.

Graves, A. H. 1949. Breeding chestnuts for timber. Jour. New York Bot. Gard. **50**: 248-254.

Heald, F. D. and Gardner, M. W. 1914. Longevity of pycnospores of the chestnut-blight fungus in soil. Jour. Agr. Res. **2**: 67-75.

——— **and Studhalter, R. A.** 1914. Birds as carriers of the chestnut-blight fungus. Jour. Agr. Res. **2**: 405-422.

Hodson, E. R. 1920. Is the American chestnut developing immunity to the blight? Jour. Forestry **18**: 693-700.

Illick, J. S. 1921. Replacement of the chestnut. Jour. Forestry **19**: 105-114.

———. 1925. Will the chestnut come back? American Forests and Forest Life **31**: 7-9.

Keever, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. Ecology **34**: 44-54.

Kendeigh, S. C. 1942. Research areas in the National Parks, January 1942. Ecology **23**: 236-238.

King, P. B. and Stupka, A. 1950. The Great Smoky Mountains—their geology and natural history. Scientific Monthly **71**: 31-43.

Korstian, C. F. 1924. The tragedy of chestnut. Southern Lumberman **117**: 180-183.

——— **and Stickel, P. W.** 1927a. The natural replacement of blight-killed chestnut. U.S.D.A. Misc. Cir. **100**, 15 pp.

——— **and** ———. 1927b. The natural replacement of blight-killed chestnut in the hardwood forests of the northeast. Jour. Agr. Res. **34**: 631-648.

Little, E. L. 1953. Check list of native and naturalized trees of the United States (including Alaska). U.S.D.A. Agr. Handbook No. **41**, 472 pp.

Metcalf, H. 1912. The chestnut bark disease. U.S.D.A. Yearbook of Agriculture **1912**: 363-372.

Nelson, R. M. 1930. Growth and mortality of chestnut sprouts. Jour. Forestry **30**: 872-873.

Nelson, T. C. 1955. Chestnut replacement in the southern highlands. Ecology **36**: 352-353.

Nicholas, H. M. 1925. What trees are replacing our chestnut? Forest Leaves **20**: 44-45.

Favari, A. 1949. Chestnut blight in Europe. Unasylva **3**: 8-13.

Pearson, R. A. (Chairman). 1912. The Pennsylvania Chestnut Blight Conference, Harrisburg, 253 pp.

Perry, G. S. 1922. The special planting problems in Pennsylvania. Jour. Forestry **20**: 507-512.

Pinchot, G. 1907. Forest planting leaflet: Chestnut. U.S.D.A. Forest Service Circ. **71**, 4 pp.

Retan, G. A. 1918. A practical reforestation policy. Jour. of Forestry **16**: 335-340.

Richards, E. C. M. 1917. A study of reforested chestnut cut-over land. Jour. Forestry **15**: 609-614.

Sargent, C. S. 1933. Manual of the Trees of North America. New York. 910 pp.

Shanks, R. E. 1954. Climates of the Great Smoky Mountains. Ecology **35**: 354-361.

Shear, C. L., Stevens, N. F., and Tiller, R. J. 1917. *Endothia parasitica* and related species. U.S.D.A. Bull. **380**, 82 pp.

Society of American Foresters. 1954. Forest Cover Types of North America (Exclusive of Mexico). Report of the Committee on Forest Types. Washington, 67 pp.

Spaeth, J. N. 1920. Growth study and normal yield tables for second growth hardwood stands in central New England. Harvard Forest Bull. No. **2**, 21 pp.

Thornthwaite, C. W. 1931. The climates of North America according to a new classification. Geog. Rev. **21**: 633-655.

Toumey, J. W. 1914. What should be done with the chestnut stands in southern New England. Soc. Amer. Foresters Proc. **9**: 38-45.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monog. **26**: 1-80.

Wilber, C. P. 1926. Is the American chestnut coming back? American Forest and Forest Life **32**: 349.

Ziegler, E. A. 1920. Problems arising from the loss of our chestnut. Forest Leaves **17**: 153-155.

SOME CLUES TO GREAT BASIN POSTPLUVIAL CLIMATES PROVIDED BY OAK DISTRIBUTIONS

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Introduction

The present distribution of floras in relation to the past histories of their individual components has long been considered important in paleoclimatological investigations. Information gained from studies of disjunct and relict floral elements through pollen analysis and through the new sciences of dendrochronology and dendroclimatology has contributed qualitative and quantitative data that have supplemented greatly the mass of physical facts regarding the nature, duration, and trends of past climates as they have related to the present. As a result, a fairly reliable chronology of pluvial and postpluvial climates has been determined.

Rarely, however, has it been possible to assemble from any source data that reflect directly on the probable seasonal characteristics of these

FIG. 1. First hybrid (Quercus gambelii x turbinnella) to be discovered in northern Utah: Harker's Canyon, Oquirrh Mountains (Mr. Rudy Drobnick stands in the center of the clone, which is 80 feet in its longest dimension).

paleoclimates compared to our own. A major purpose of this report, therefore, is the presentation and analysis of climatic data made possible by the recent discovery of a hybrid oak within the Great Basin that lends certain implications regarding the detailed temperature features of the Postpluvial's Altithermal age.

ACKNOWLEDGMENTS

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To present the comparative temperature features of the problem, on which so much of the discussion rests, would have been impossible without the unusual interest and attention contributed to the study by several friends who attended the recording thermographs in southern Utah and northern Arizona. Grateful appreciation is extended to Mrs. Viola Kelsey, New Harmony, Utah; Mrs. Verdna Gregerson, Pintura, Utah; Mr. and Mrs. Rex McArthur, Glendale, Utah; Mr. A. H. Woodbury, Kanarraville, Utah; and Superintendent John Riffey, Grand Canyon National Monument. We are indebted to Ernst Antevs for critically reading the manuscript and offering a number of helpful suggestions.

THE NATURE OF THE PROBLEM

In the spring of 1954 a large clone of scrub oak possessing characters strikingly different from those of the Gambel oak of north-central Utah was discovered on the foothills of the Oquirrh Mountains (Fig. 1), twenty miles west of Salt Lake City, by Rudy Drobnick, a graduate student in the Department of Botany, University of Utah. Subsequently Cottam and Drobnick (1955) reported several additional colonies of this new oak on both the east and west slopes of the Oquirrh Mountains, on the Traverse Mountain spur connecting the Oquirrh and Wasatch mountains, and at many discontinuous localities along the lower mountain slopes of the Wasatch escarpment and other orographic systems constituting the eastern boundary of Pluvial Lake Bonneville of the Great Basin (Fig. 2).

Specimens of the new oak were determined by Cornelius H. Muller to be a hybrid of the common Gambel oak, *Quercus gambelii* Nutt. and *Q. turbinella* Greene, an evergreen shrub whose main distribution is farther to the south in central Arizona. This identification was later confirmed by John M. Tucker, who in the summer of 1955

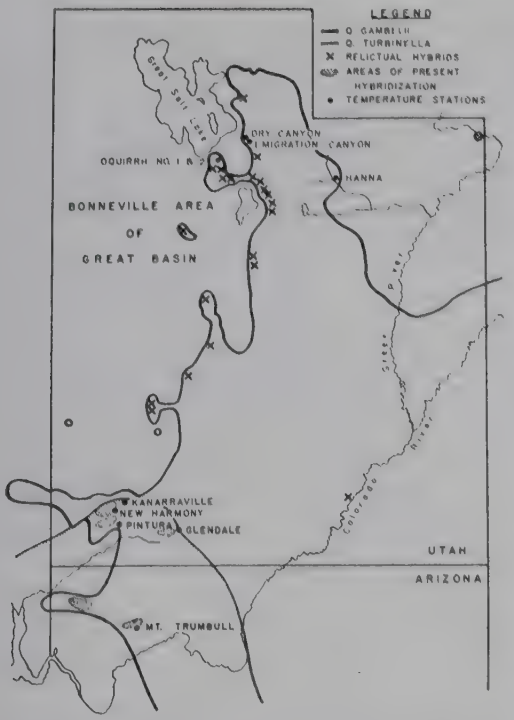

FIG. 2. Map of Utah and northern Arziona showing hybrid locations, distributions of the parental species, and temperature stations.

joined W. P. Cottam in an intensified field study of this problem.

Since the most northerly clones of this oak hybrid are separated by some 260 miles from the present northern limits of *Q. turbinella,* near the Pine Valley Mountains of southwestern Utah and slightly north of the southern rim of the Basin, a past, extensive distribution of *Q. turbinella* northward along the eastern margin of the Great Basin seems virtually certain.

Major questions in this phytogeographic riddle are these: At what epoch of geologic time could this heat-requiring live oak, *Q. turbinella,* have entered the Great Basin and migrated north as far as the Great Salt Lake to consort freely with the common Gambel oak, *Q. gambelii,* and to leave living hybrids as unmistakable evidence of its past expanded distribution? Could this migration have antedated the last major period of ice advance in the Wasatch Mountains?

These questions will be considered in due time, but it will be enlightening to consider first something of the ecology and distribution of both parental species, as well as the hybrids.

ECOLOGY AND DISTRIBUTION

Quercus turbinella is an evergreen shrub, or rarely a small tree, with small, gray-green, spinose-toothed leaves (Fig. 3, A). Typically it occurs in semi-arid chaparral or pinyon-juniper woodland. Its range extends from central California southward to northern Baja California, and eastward to west Texas. It attains perhaps its greatest abundance in central Arizona, where it may form extensive areas of chaparral, commonly at elevations from 3500 to 6000 feet (or higher on open, south-facing slopes). It extends northward into Utah, but occurs only in the southwestern part of the State.

Quercus gambelii is a deciduous shrub or small tree with medium-sized green leaves that are moderately to deeply lobed (Fig. 3, C). This species is the one widely distributed oak in the central and southern Rockies in the ponderosa pine zone. Its range extends from southern Wyoming southward into northern Mexico. In the Wasatch, where ponderosa pine is almost completely lacking, Gambel oak often forms a nearly continuous belt from about 5500 to 7000 feet elevation. It reaches its northern limits in Utah approximately 45 miles north of Salt Lake City and two miles south of Brigham City. In the mountain valleys east of here its northernmost outposts are on a low divide separating Ogden's Hole from Cache Valley, and along the fields of Mantua, a small settlement east and slightly north of Brigham City, Utah.

Relictual Hybrids within the Great Basin

The hybrids (Fig. 3, B) are, in general, morphologically intermediate between the two parental species. In leaf persistence, also, they are intermediate, their leaves remaining green till late fall—long after *Q. gambelii* has dropped its leaves. The leaves then die and turn brown, but remain on the shrub till spring. Those along the Wasatch front are situated near and slightly above the Bonneville shore line at approximately 5200 feet elevation. One cluster occurs at an elevation of 4600 and the upper extreme thus far observed is 6700 feet. In the Oquirrh range and on desert ranges of the Basin south, the average elevation of the hybrids is higher.

The optimal range of *Q. gambelii* within the Great Basin is from 500 to 1000 feet above the hybrid clones. Here in favorable sites Gambel oak occurs as solid and extensively continuous thickets, while at the altitude of the hybrids discrete colony formation is the rule. Such colonies, like those of the hybrids, are sharply discontinuous. One usually observes remarkable morpho-

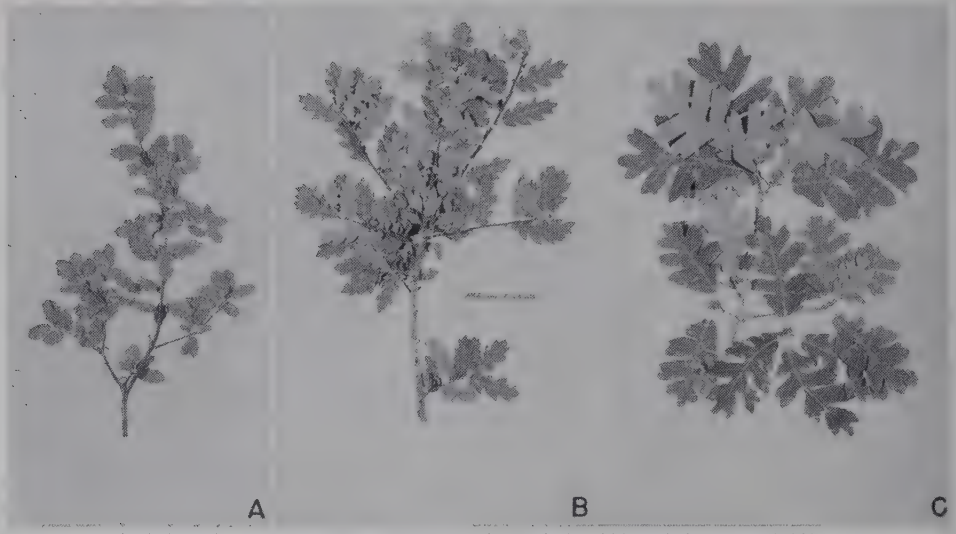

FIG. 3. The hybrid (B) with the parental species: *Q. turbinella* (A) and *Q. gambelii* (C).

logical uniformity in each such colony. In a species as variable as Gambel oak, this fact alone would strongly suggest that a "colony" is actually a single individual clone which has increased in size by vegetative proliferation. Evidence of the validity of this assumption comes from a recent experiment by Pendleton (1952) in which the radioactive tracer P 35, injected into an oak rhizome at one point in a large colony, revealed that practically the entire colony was connected, thus showing it to be almost entirely the product, through clonal development, of a single acorn. By their appearance, young oak clumps suggest development through proliferation from a plant produced by a single acorn. The presence of progressively smaller clones of Gambel oak below the hybrids, therefore, seems to warrant the conclusion that this species has definitely increased its range downward during the period of our present climatic regimen.

The hybrids commonly occur on south-facing slopes, while Gambel oak at comparable altitudes occurs more abundantly on cooler, less exposed slopes. Significant also is the fact that Gambel oak migration below the Bonneville level is confined to habitats such as the north-facing slopes of ravines, gentle depressions of particularly deep and well-watered soils of bench lands, and areas along water courses that issue from the mountain ranges. These are habitats which, though presenting similar elevations to those of the hybrid clones, stand in marked contrast to them, the ones offering coolness and moisture, the others heat and drought.

Several facts suggest that some, if not most, of the hybrid clones may have grown from the original acorns of the hybrid cross (i.e., they are F_1's): (1) as stated above, most of them are more or less directly intermediate morphologically between the two parental species, (2) they commonly occur as rare, isolated individual clones, rather than as groups or colonies of clones, and (3) more than three years of study seem to warrant the conclusion that many of them are highly sterile. It is our opinion that such clones may well be very old—perhaps as much as 4000 years old—if a chronology of the postpluvial (to be discussed later) is correct. The very large size of the largest of them (some clones are more than 200 feet in length) would be in keeping with this opinion.

Alternative hypotheses to account for these northern hybrids without the actual northward migration of *Q. turbinella* could be advanced, but those which have occurred to us seem untenable.

Migration of the actual hybrids, themselves, need scarcely be considered seriously. The original hybrid, of course, would not migrate; rather, migration would be effected by the dispersal of its acorns or pollen. A northward march of the order of 250 miles would probably require many generations, and after only a few repeated back-crosses to the recurrent parent, *Q. gambelii*, the *Q. turbinella* influence in the descendants would be so

dilute that they would be virtually indistinguishable from pure *Q. gambelii.*

The possibility of the origin of the hybrids through long-range pollination cannot be dismissed so easily, perhaps, but this explanation, also, seems to us highly improbable. First of all, the conditions necessary for long-range pollination would be these: (1) coincidence in the time of flowering between *Q. gambelii* along the Wasatch and *Q. turbinella* 250 miles or more to the southward, (2) wind currents at the time of pollination sufficiently strong and sustained, and in the right direction—in general, from south to north—to transport pollen from southwestern Utah to the region of the present hybrid locations on the Oquirrhs and Wasatch, and (3) viability of the pollen of *Q. turbinella* after the desiccating effects of this long wind-borne journey. Assuming, for the sake of discussion, that these conditions might have been met on occasion, it would appear, nevertheless, that such long-range pollination would be ineffective. The mere presence of *Q. turbinella* pollen would not be enough, inasmuch as *Q. gambelii* pollen would also be present, and in abundance. Fertilization would probably be effected by the latter. Whatever the reason may be—perhaps a difference in rate of pollen tube growth—apparently fertilization of a pistillate flower is better effected by pollen of the same species than by that of a foreign species in cases where pollen of both may be present. This may be inferred from the following facts: (1) hybrids between two distantly related oaks (as in the present case) are rarely, if ever, encountered in areas where both species are equally abundant, but (2) have usually been observed in areas where one is abundant but the other is represented by only a few isolated individuals. We have observed this repeatedly in the present study. E. J. Palmer, a life-long student of oaks and their hybrids, remarked (1948) on this phenomenon, also, explaining it as follows: "the chance of the rare plant being pollinated by one of its own kind is small or nonexistent, except in so far as it may be effected by self-pollination. On the other hand, the chance of its pistillate flowers being fertilized by the wind-borne pollen of the dominant species is very great. In the case of a hybrid found under such circumstances it may almost be assumed that the rare species was the mother plant". Thus, in the case of *Q. gambelii* along the Wasatch, the presence of an abundance of pollen from shrubs of the same species nearby would virtually insure fertilization even if we assume that on rare occasions small amounts of *Q. turbinella* pollen might reach the area.

Thus, the most probable explanation in our opinion would be that the hybrids were formed precisely where they are now found, as the result of direct crossing between *Q. gambelii* and *Q. turbinella* at some time in the past when the range of the latter actually extended at least as far north as the northernmost of the existing hybrids. Since the hybrids, in general, occupy warmer and drier sites than *Q. gambelii,* it would seem logical that *Q. turbinella* must have occupied still warmer sites. A logical inference, therefore, would be that in the period when *Q. turbinella* advanced along the foothills constituting the eastern limits of the Basin, the climate was definitely warmer and presumably drier than at present.

Areas of Present Hybridization

It was assumed that a clearer picture of the precise relationships of the two parents and the hybrids that were supported by this climate of the past in the Great Basin could be ascertained by locating an area where *Q. turbinella* and *Q. gambelii* exist in juxtaposition today and are hybridizing as they did in this more ancient time. Accordingly, after some preliminary exploration, the areas of the Pine Valley Mountains in southwestern Utah and certain mountains in northern Arizona north of the Grand Canyon (the "Arizona Strip") were selected for concentrated study.

The results exceeded our fondest expectations. On the east slope of the Pine Valley Mountains, at Long Valley east of Zion National Park, at Black Rock Mountain on the "Arizona Strip" 30 miles northeast of Lake Mead, and at Mount Trumbull near Grand Canyon National Monument both parents were found, and many hybrids of both recent and ancient origin occur in ecotonal areas between the parental habitats (Fig. 2). The altitudinal range of these hybrids varies from extremes of approximately 5000 feet to 7000 feet—just as they occur in the Great Basin. At the lower extremes of altitude, *Q. gambelii* is found only rarely on the north-facing slopes of ravines, or on sharp projecting cliffs. At 7000 feet on Mt. Trumbull, *Q. turbinella,* in turn, appears restricted to the steep, south-facing slopes of a black lava formation. Commonly the hybrid is found in circumstances where one of the parents is relatively rare and the other occurs in much greater abundance. These hybrids differ in no important respect from, and present much the same range of forms as, the relictual northern hybrids in the Great Basin.

Explanation of Oak Distribution on the Basis of Postpluvial Chronology

Now let us consider the question raised earlier as to the period in past geologic time when *Q. turbinella* could have made its northward migration. It would seem that any period during which climate was colder than at present, such as any of the major glacial periods, would certainly be ruled out. This species reaches its northern limits today in extreme southwestern Utah. Since (a) it does occur north of the obvious topographic barrier of the Great Basin divide (locally, near New Harmony), but (b) we know of no evidence that it is presently extending its range northward, it seems fair to assume that climatic factors are limiting. Since it is not surviving in more northerly areas today, where the presence of its hybrids bears testimony to its occurrence in the past, it seems quite improbable that it could have weathered the even more rigorous climate of the several Wisconsin maxima. Furthermore, as mentioned above, it seems logical to infer that the climate during the northern sojourn of *Q. turbinella* was even warmer and drier than at present. The improbability of its having survived the Wisconsin maxima is apparent when one considers evidence that renders it doubtful that even the hardier Gambel oak, itself, persisted along the Wasatch during the Wisconsin period.

At its upper altitudinal limits, Gambel oak, as a continuous belt or zone, occurs today at about 7000 feet elevation (depending on slope exposure), where it meets the spruce-fir belt. From the lower extensions of the oak belt to the *Picea pungens—Abies concolor* zone of the spruce-fir belt of the Wasatch Mountains, there is an altitudinal differential of approximately 2500 feet and an annual mean temperature difference of nearly 8° F. To the *Picea engelmanni—Abies lasiocarpa* zone of the upper spruce belt there is an additional differential of a thousand feet, and the temperature difference from the lower oak belt probably exceeds 11° F. These facts are important for their approximation of the mean temperature differences between the present climate and the Cary maximum of ice advance in these mountains, a culmination dated by Antevs (1955) at about 24,000, by Eardley et al. (1957: 1198) at roughly 35,000, and by Suess (1956) by means of radiocarbon at about 14,000 years ago. Antevs (op. cit.) estimates a July mean difference of 12° F.—a climate that would certainly have shifted the Engelmann spruce-alpine fir zone downward to the shores of ancient Lake Bonneville.

The Bonneville Lake area is notable for the paucity of fossil flora and most fauna, but in 1957 Professor Daniel J. Jones of the Department of Geology, University of Utah, uncovered excellent impressions of leaves and twigs of the alpine fir (*Abies lasiocarpa*)[1] imbedded in a matrix of clay and ostracod shells. The nature of this matrix, together with its position in an old, shallow embayment of the lake, according to Professor Jones, virtually assures that these leafy twigs had their origin from trees that grew along the shores of Lake Bonneville at a time when the lake level stood well below the Provo stage. Thus there seems to be little doubt that, in pluvial times of the postglacial, spruce-fir forest occupied the area now claimed by oak. Under such conditions of climate, and with Lake Bonneville filling the valleys below, places of refuge for *Q. gambelii* in north-central Utah must have been exceedingly rare if not nonexistent.

With the onset of postpluvial warmth, a general shift upwards of all vegetational belts most likely resulted, and the migration northward of Gambel oak along the lower altitudes of the Wasatch front would have been possible. The present northern limits of this species in Utah were doubtless reached after the disappearance of the last major ice accumulation in the Wasatch Mountains. Furthermore, it seems to have reached its limits of tolerance for climatic factors at these northern limits, some 45 miles north of Salt Lake City. Observable winter damage to the colonies of Gambel oak situated at these northern outposts is strong presumptive evidence of occasional minimum temperatures exceeding the tolerance limits of this species. Historical records seem conclusive of no northward movement in a century and a quarter of time, and careful reconnaissance of the Wasatch Mountains north of this point reveals no evidence of a more northerly extension of Gambel oak.

Considering, then, the thermal requirements of the two parental species and hybrids, together with their present distribution as outlined above, an explanation requires a postglacial sequence of climatic events essentially as follows: (1) a period of increasing warmth and moisture decline, which would account for the gradual shift upward of the spruce-fir belt and its replacement along the old shore line of Lake Bonneville by the northward migration of *Q. gambelii;* (2) a period marked by a climatic regimen warmer and presumably drier than the present and of sufficient duration to permit the migration of *Q. turbinella* as far north as the Great Salt Lake along a narrow altitudinal belt contiguous with, but in general

[1] Kindly determined for us by H. D. MacGinitie.

below that of, the Gambel oak; (3) a third and more recent trend sufficiently cold to have exterminated the live oak parent in the Great Basin but to have left the more cold-enduring hybrid associated at low elevations with *Q. gambelii*.

Such a chronology of postglacial climates fulfilling all the major requirements of oak distribution within the Great Basin has indeed been revealed during the past few decades. Numerous workers in Europe and America in many fields of research have contributed to this knowledge. Included as evidence for dating and assessing the nature of climatic change are facts of varve chronology (DeGeer 1940), glacial expansion and recession (Matthes 1939), stream deposition and erosion (Bryan and Albritton 1943), mud-rock flows (Williams 1956), lake fluctuations (Gilbert 1890, Gvosdetsky and Hawkes 1953), lake desiccation and rebirth with subsequent salt accumulations (Eardley, Gvosdetsky and Marsell 1957, Gale 1914, Van Winkle 1914), carbon 14 determinations (Libby 1951), dendrochronological data (Douglass 1940), pollen analysis (Hansen 1947, Sears 1948), and anthropological studies (Jennings 1957).

According to Antevs (1955, 1948, 1952), whose dating of postglacial events in the Great Basin are correlated principally with varve chronology of Europe and eastern North America and with the saline content of various lakes of southern Oregon and Nevada during Medithermal time, the last maximum extension of glaciation in the Wasatch Mountains was attained during the Cary Maximum, approximately 24,000 years ago. From then until about 12,000 years past, temperature had gradually risen from a July mean of about 12 degrees below our present July temperature to that approaching our present climate. Then the temperature dropped. The subsequent marked temperature rise, which began some 10,000 years ago, marked the end of the glacio-pluvial age and the beginning of the postpluvial or "Neothermal" age of Antevs. He divides the Neothermal age into three distinct periods according to temperature characteristics. The first, or Anathermal, period began with mean temperatures slightly below our present climate and with moisture somewhat higher. Temperature, however, took a rather sudden upturn, and at the beginning of the second, or Altithermal, period 7500 years ago, temperature had risen above our present climate, and the "Long Drought" lasting 3500 years was on. During this time Abert and Summer lakes in south-central Oregon, Owens Lake in east-central California, Winnemucca and Walker lakes in Nevada all suffered complete desiccation (Antevs 1952, Eardley et al. 1957), and their salt accumulations were buried under fresh alluvium and/or dispersed by wind. Glaciers from the Canadian Rockies to Timpanogos in the Wasatch in Utah completely disappeared and many of our canyons experienced mud-rock flows (Williams 1956). Temperature at the height of the Altithermal is estimated to have approached four degrees F. above that of the present climate.

While most authorities are in basic agreement on the general nature and sequence of these climatic events of the postpluvial, they differ somewhat on the details of chronology and especially on nomenclature. Deevey and Flint (1957) propose the term "Hypsithermal Interval" to designate that period of the postpluvial when temperatures exceeded the present. Their "Hypsithermal Interval" extends from approximately 7000 B.C. to 600 B.C., while Antevs' "Altithermal" covers the period from about 5500 B.C. to 2000 B.C.

The present or Medithermal climate according to Antevs, which began about 4000 years ago, is approximately equivalent in time to the *Little Ice Age* of Matthes (1939). Temperature is believed to have dropped around four degrees F., the glaciers of the Western mountains reappeared, and the lakes of Oregon, California and Nevada were reborn. Sharp droughts during our present period, as we are all aware, are recurrent, and one reported by Douglass (1940) lasting from 1276-1299 was disastrous to the red man of the Southwest. But no drought of the Medithermal has been so severe or of such long duration as to desiccate lakes. Conversely, short periods of excessive precipitation are also known to have occurred through the Medithermal period.

This brief account of the historical aspects of the Neothermal age thus provides a succession of climates admirably suited to explain the riddle of oak distribution within the Great Basin. The warm, moist climate of the Anathermal furnished ideal conditions for a rapid migration of Gambel oak, and the great warmth of the Altithermal period provided the only possible conditions for the Basin migration of the live oak, *Q. turbinella*. In Medithermal times a return to a climate cool enough to regenerate glaciers in high mountains could well have been sufficient to exterminate the live oak, yet warm enough at the base of these ranges to have spared the hybrid.

Temperature Data and Analyses

Careful reconnaissance established the northernmost clone of the hybrid to be located just north of Weber Canyon, 25 miles north of Salt Lake City. At approximately five miles south of

the Great Salt Lake on both east and west slopes of the Oquirrh Mountains, and one mile north and twenty miles east of the southeast limits of the Great Salt Lake on the west escarpment of the Wasatch Mountains, are several clones convenient for intensive study. Since we assume that *Q. turbinella* must have been present in the vicinity at each of these locations for the hybrids to have been produced, it is felt that the former must have occurred at least as far north in Altithermal times as the northernmost Wasatch hybrids.

It was assumed, therefore, that the logical procedure for ascertaining the possible thermal characteristics of the Altithermal climate lay in a direct comparison of the present seasonal temperature regimen prevailing at these northern outposts of hybrid oak distribution with data simultaneously gathered at the most northerly point along the ancient migratory route where present hybridization still occurs. Such data should provide: (1) some indication as to the thermal requirements of *Q. turbinella* and the hybrids, and (2) some basis for reconstructing important features of the Altithermal paleo-climate.

The question might be raised as to whether or not we are dealing with really comparable entities when we compare present-day *Q. turbinella* of the New Harmony area, for example, with the species as it existed at the latitude of Salt Lake City during the Altithermal period. In other words, how do we know that the species has not undergone significant evolutionary change since that period? As far as morphological change is concerned, this brief span of time seems quite insignificant, for evolution in many oak lineages (judging by fossil leaf impressions) has been remarkably slow. This is certainly the case with *Q. turbinella,* itself, for leaf impressions of its Tertiary equivalent, *Q. dispersa* (Lesquereux) Axelrod,[1] are known from floras as old as the Middle Miocene Tehachapi Flora of southern California (Axelrod 1939). Similarly, the modern *Q. dunnii* Kellogg (*Q. palmeri* Engelmann) is known, through its Tertiary equivalent, *Q. Pliopalmeri* Axelrod, from the same flora.

In the Tehachapi flora *Q. turbinella* was associated with an assemblage of chaparral or xeric woodland species whose modern equivalents are frequently associated with it today—pinyon pine, *Berberis (Mahonia) fremontii, Quercus dunnii, Cercocarpus betuloides,* etc. Thus, *Q. turbinella* would seem to have undergone little ecological change since Middle Miocene.

This is not to say, of course, that a widespread species such as *Q. turbinella* might not undergo some physiological differentiation from one area to another, such as McMillan (1957) has shown in *Q. macrocarpa* in Nebraska. For example, one would scarcely expect to find the same degree of winter hardiness in populations of *Q. turbinella* at its lower altitudinal limits (e.g., between Leeds and Anderson Junction, Washington County, Utah) at around 3,000 feet, as on Mt. Trumbull at 6,300 feet. However, when we compare Altithermal *Q. turbinella* of the Salt Lake area with the present-day species at New Harmony, we are presumably dealing with the northernmost populations of the species in both cases. For this reason, and from what we know of the generally slow rate of morphological and ecological change in the species, it would probably be safe to assume that *Q. turbinella,* in general, has undergone little if any significant evolutionary change since the Altithermal period.

Procedure

Accordingly, eight recording thermographs were set up in early March, 1956, at stations throughout the region considered most likely to provide the data needed to achieve the two objectives mentioned above. "Tempscribes" (Bacharach Industrial Co.), provided with 8-day clocks and weekly charts with temperature range +110° to −30° F., were used. The instruments were suspended from horizontal crossbars firmly anchored in the axils of branches 4-6 feet above the ground. Above the thermographs, and with the crossbar serving as a ridgepole, white canvas tents were arranged in such a manner as to provide good air circulation and complete protection from direct sunlight and precipitation. Continuous temperature records were secured for a period of one year (March, 1956-March 21, 1957). Each Tempscribe was checked against a standard mercury thermometer once weekly.

Stations (Fig. 2)

1. Oquirrh No. 1, at an altitude of 5760 feet, is situated on a southwest-facing slope near the bottom of Harker's Canyon about three miles west of Bacchus on the northeastern foothills of the Oquirrh Mountains. The large clone of hybrid oak, more than 75 feet in length, is surrounded by scattered clones of *Q. gambelii.* Less than fifty feet to the south, in the bottom of the canyon and on the cooler north-facing slopes, are tall and continuous thickets of the Gambel oak.

[1] *Q. dispersa* was originally regarded as a Tertiary equivalent of the modern *Q. dumosa* Nutt., which is very closely related to *Q. turbinella.* More recently Axelrod has considered it to be nearer *Q. turbinella* (written communication).

2. Oquirrh No. 2 has an altitude of 5760 feet on the northeast-facing slope of Harker's Canyon approximately 100 feet south of Station No. 1. This station was not established until September 23, 1956. It was particularly designed to provide information on the effects of slope exposure on temperature in contrast to Station No. 1. It is located in the midst of a tall oak thicket of *Q. gambelii.*

3. Dry Canyon Station, at an altitude of 5280 feet, is located in a hybrid clone on the southwest exposure of the Wasatch escarpment at the mouth of Dry Canyon one-half mile northeast of the University of Utah Administration Building. This hybrid clone is surrounded on the west, north, and east by numerous clones of *Q. gambelii* and on the south by Palouse prairie.

4. Emigration Canyon Station has an altitude of 5800 feet on a southwest exposure of a secondary ridge near the summit of Little Mountain, 8 miles east of Salt Lake City. This station is located in tall thickets of Gambel oak in the lower altitude of the continuous oak belt.

5. Kanarraville Station has an altitude of 5441 feet and is located in the small town of Kanarraville, Iron County, Utah, on a gentle westerly slope at the foot of the Hurricane escarpment along which *Q. turbinella* is presumed to have migrated into the Great Basin. The station is established on the divide between the Colorado River drainage and Great Basin. Gambel oak frequents the area. The instrument was suspended in an elm tree for convenience.

6. The station at New Harmony has an altitude of 5290 feet. This station, considered of particular importance to this study, is located at the northwest end of the small community of New Harmony, Washington County, Utah. Numerous colonies of *Q. turbinella* and *Q. gambelii* surround the community, and a great array of hybrids and apparent backcrosses abound. The station is separated in a southwesterly direction by only 8 miles and is 151 feet lower in elevation than the Kanarraville station. For convenience the instrument was suspended in an apple tree on the lot of Verl Kelsey.

7. The Pintura station, at an altitude of 4175 feet, is located in a dense thicket of *Q. turbinella* in a narrow valley separating the Pine Valley Mountains on the west from the Hurricane fault on the east. Here the live oak reaches its maximum expression in Utah. The station is ten miles south of New Harmony.

8. Glendale, a small community situated in Long Valley, Kane County, Utah, has an altitude of 5824 feet. The station marks the northernmost occurrence of *Q. turbinella* and the hybrids in the valley. The predominant vegetation here is Gambel oak and ponderosa pine. For convenience the instrument was suspended in a peach tree.

9. Mt. Trumbull, at the base of which this station was established, is situated in northwestern Arizona, on the "Arizona Strip," approximately 75 miles south of Pintura, Utah, at an elevation of 6300 feet. The station area, with a southwest exposure, harbors scattered clones of *Q. turbinella* and the hybrid and large representations of Gambel oak and ponderosa pine. The instrument was suspended in a clone of *Q. turbinella.*

10. Hanna, at an elevation of 6800 feet, representing the upper limits of the optimal Gambel Oak Zone, is located on the west fork of the Duchesne River in the southwestern section of the Uinta Mountains, 60 miles southeast of Salt Lake City. No recording instrument was located here, and the data given are from maximal and minimal temperatures from U. S. weather reports.

Results

The weekly charts of continuous temperature recordings provided comparative data from which several analyses were made for the various aspects of temperature prevailing at the locations considered most significant: (1) the northern relictual hybrid locations in the Great Basin, (2) the northernmost locations where *Q. turbinella* and *Q. gambelii* are hybridizing at present, (3) an area where *Q. turbinella* reaches its optimal development, and (4) an optimal location for *Q. gambelii.*

Table I gives in detail the basic data used for the construction of most of the graphs as well as for the conclusions reached regarding the various oak species' temperature requirements and tolerances. Table I provides also the data from which the implications regarding the probable temperature aspects of the Altithermal paleoclimate are determined. Daily and weekly minimum, maximum, and mean temperatures were determined for each station, but it was found desirable to present in Table I thirteen four-week periods of averages for the minimum, maximum, and mean. This allowed for a simplification of the charts based on Table I by "smoothing out" the fluctuating curves produced by great daily and weekly variations in temperature without sacrificing the significant seasonal trends. The year's averages of the minimum, maximum, and mean temperatures are also given for each station in Table I as well as their individual departures from the New Harmony temperature.

TABLE I. Minimum, maximum, and mean temperatures by four-week periods for all stations for one year: March, 1956 to March, 1957

	Station	Mar 21 Apr 17	Apr 18 May 15	May 16 Jun 12	Jun 13 Jul 10	Jul 11 Aug 7	Aug 8 Sep 4	Sep 5 Oct 2	Oct 3 Oct 30	Oct 31 Nov 27	Nov 28 Dec 25	Dec 26 Jan 22	Jan 23 Feb 19	Feb 20 Mar 19	Year Ave.	Departure from New Harmony	
1	Dry Canyon	38.3	46.6	58.4	62.5	66.2	63.4	60.6	45.0	31.1	28.3	26.1	28.9	37.8	45.7	+ 3.6	
	Oquirrh #1	31.3	41.0	49.2	52.9	57.9	50.0	50.4	41.1	27.4	23.5	20.9	22.8	32.6	38.5	− 3.6	
	Oquirrh #2								38.8	22.3	22.2	19.6	17.4	30.1			
3	Emigration	32.6	41.5	50.0	51.4	56.7	53.2	49.6	41.4	27.0	21.1	20.4	21.3	30.4	38.2	− 3.9	
4	Kanarraville	30.8	42.1	50.0	58.2	62.2	61.7	54.0	42.3	21.5	20.7	24.0	25.1	33.8	40.5	− 2.0	
	New Harmony	34.7	43.7	52.7	58.8	61.3	57.9	55.0	41.7	26.2	25.1	26.6	28.1	35.6	42.1	000	
2	Pintura	38.8	48.4	55.5	63.8	64.3	62.2	58.7	46.8	33.0	29.9	30.9	31.8	40.4	46.5	+ 4.4	
	Glendale	30.4	36.1	47.3	50.9	54.8	50.4	49.8	38.2	26.0	24.4	26.1	26.2	33.0	38.0	− 4.0	
5	Mt. Trumbull	32.4	40.4	48.8	54.6	59.2	58.2	53.8	39.2	26.5	25.0	27.2	25.3	32.2	29.6	− 2.5	
	Hanna	23.8	31.2	41.3	41.4	47.3	41.9	38.9	29.5	15.4	8.1	7.6	6.8	23.7	27.5	−14.6	
																	Minimum
	Dry Canyon	57.6	66.3	81.8	86.5	92.2	87.2	81.9	63.0	46.2	41.2	38.3	43.1	51.5	64.4	− 4.5	
	Oquirrh #1	59.9	68.1	82.8	87.2	92.4	88.8	85.8	65.4	46.1	41.4	40.7	44.9	52.9	65.9	− 4.0	
	Oquirrh #2								59.3	39.2	34.8	35.9	36.3	47.2			
3	Emigration	56.2	64.4	79.3	80.8	86.2	83.8	79.9	63.9	46.0	38.3	39.8	43.1	48.4	62.3	− 7.6	
4	Kanarraville	59.2	65.7	79.9	85.4	85.1	84.7	82.4	67.1	55.3	48.9	45.6	46.9	54.2	66.7	− 3.7	
	New Harmony	63.5	69.9	83.3	89.8	88.6	87.4	86.5	70.4	58.7	51.1	51.4	52.1	56.5	69.9	000	
2	Pintura	68.7	75.0	91.7	98.7	98.0	97.4	92.2	76.5	58.5	52.2	53.4	57.1	61.7	75.5	+ 5.6	
	Glendale	63.7	68.6	82.3	87.5	86.1	86.1	82.8	69.1	57.8	51.9	47.8	52.7	55.0	68.6	− 1.3	
5	Mt. Trumbull	59.7	66.4	81.0	86.6	87.9	88.3	84.4	65.7	57.1	52.2	47.7	49.7	52.0	67.6	− 2.3	
	Hanna	52.3	59.9	73.6	77.5	79.5	76.5	74.4	60.3	43.4	35.5	32.2	32.8	43.5	57.0	−12.9	
																	Maximum
	Dry Canyon	47.9	56.4	70.1	74.5	79.2	75.3	71.2	54.0	38.6	34.7	32.2	36.0	44.6	55.0	− 1.0	
	Oquirrh #1	45.6	54.5	66.0	70.0	75.1	69.4	68.1	53.2	36.7	32.4	30.8	33.8	42.7	52.2	− 3.8	
	Oquirrh #2								49.0	30.8	28.5	27.7	26.8	38.6			
3	Emigration	44.4	52.9	64.6	66.1	71.4	68.5	64.7	52.6	36.5	29.7	30.1	32.2	39.4	50.0	− 6.0	
4	Kanarraville	45.0	53.9	64.9	71.8	73.6	73.2	68.2	54.7	38.4	34.8	34.8	36.0	44.0	53.3	− 2.7	
	New Harmony	49.1	56.8	68.0	74.3	74.9	72.6	70.7	56.5	42.4	38.3	39.0	40.1	46.0	56.0	000	
2	Pintura	53.7	61.7	73.6	81.2	81.1	79.8	75.9	61.6	45.7	41.0	42.1	44.4	51.5	61.0	+ 5.0	
	Glendale	47.0	52.3	64.8	69.2	70.4	68.2	66.3	53.6	41.9	38.1	36.9	39.4	44.0	53.3	− 2.7	
5	Mt. Trumbull	46.0	53.4	64.9	70.6	73.5	73.2	69.1	52.4	41.8	38.6	37.4	37.5	42.1	53.6	− 2.4	
	Hanna	38.5	45.5	57.4	59.4	63.4	59.2	56.6	44.9	29.4	21.8	19.9	19.8	33.6	42.4	−13.8	
																	Mean

New Harmony was selected as the station with which these basic comparisons were made because it represents the most northerly point along the probable route of migration where *Q. turbinella* occurs at present with its hybrids. Judging from the small size, but fairly large number of hybrid clones, *Q. gambelii* and *Q. turbinella* are freely consorting at the present time in the New Harmony area. Hence it seems logical to assume that the present temperature regimen at New Harmony should approach that which must have prevailed in the Salt Lake area when oak hybridization occurred. Therefore, the seasonal and annual differences between the temperature of the northern relictual hybrid stations of the Bonneville Basin and the New Harmony station should indicate the nature and degree of temperature change that must have occurred in order to produce our present climate in the Salt Lake area. The following charts will help to portray graphically these differences.

The graphic representations of the seasonal march of temperature for the most significant locations appear in Figure 4. Each line except 3 represents the combined average temperature taken for the various altitudinal extremes of each oak belt. The temperature features expressed by line 3 are obtained from one station only (Pintura, altitude 4175 feet), but because of its mid-altitudinal position and the maximal growth expression of *Q. turbinella* found there, it is presumed that this temperature represents the near average for this species and is comparable to the other oak species data.

The temperature expressed by line 1 gives the average for two stations, Dry Canyon and Oquirrh, representing the approximate 500-feet altitudinal differential marking, in general, the hybrid belt in the Great Basin. Line 2 is the average for three stations: New Harmony representing the lower altitudes, with Glendale and Mt. Trumbull, respectively, contributing data at upper elevations over the 1000-foot spread where both parents and hybrids occur. Line 4 gives the temperature averages for two stations, Emigration Canyon and Hanna, within the Gambel oak belt of approximately 1000 feet spread that marks the rather continuous thicket aspect of oak distribution in the Wasatch and western Uinta Mountains. Below the Emigration Canyon station of 5800 feet, and above the Hanna station of 6780 feet, *Q. gambelii* extends its distribution in pro-

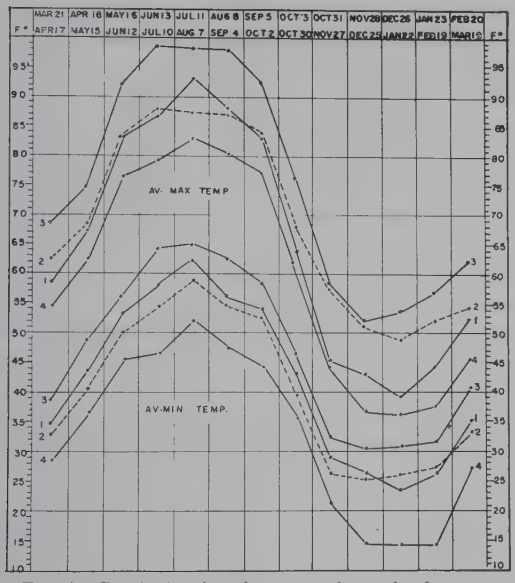
MAR 21 APR 16 MAY 16 JUN 13 JUL 11 AUG 8 SEP 5 OCT 3 OCT 31 NOV 28 DEC 26 JAN 23 FEB 20
APR 17 MAY 15 JUN 12 JUL 10 AUG 7 SEP 4 OCT 2 OCT 30 NOV 27 DEC 25 JAN 22 FEB 19 MAR 19
AV. MAX TEMP
AV-MIN TEMP.

FIG. 4. Graph showing the seasonal march of temperatures for various significant oak locations: *Line 1*—Temperature averages of two relictual hybrid stations: Oquirrh No. 1 and Dry Canyon. *Line 2*—Temperature averages of three stations supporting both parents and hybrids: New Harmony, Glendale, and Mt. Trumbull. *Line 3*—Temperatures for Pintura station supporting maximum growth of *Q. turbinella*. *Line 4*—Temperature averages for two stations supporting Gambel oak: Hanna, at upper limits of continuous belt, and Emigration, at lower limits.

gressively discontinuous fashion for about 500 feet in altitude in both directions.

Table II supplements the seasonal aspect of temperature shown in Figure 4 by giving the year's average of the maximum, minimum, and mean for each of the four significant areas.

TABLE II. Average maximum, minimum, and mean temperatures for one year (1956-57) for four significant areas

Area	Alt. Range (Approx.)	Av. Max. Temp.	Av. Min. Temp.	Av. Mean Temp.
Northern Areas of Ancient Hybridization	500	65.1	42.1	53.6
Northernmost Areas of Present Hybridization	1000	68.7	36.6	52.6
Q. turbinella	2000	75.5	46.5	61.0
Q. gambelii	2000	59.6	32.8	46.2

Considering the altitudinal positions of the various locations, the significantly warmer character throughout the year of the optimal *Q. turbinella* habitat and the colder character of the *Q. gambelii* belt in relation to both the zone of present-day hybridization in southern Utah and northern Arizona and the northern relictual hybrid sites of the Great Basin, the temperature trends depicted in Figure 4 conform rather well to general expectations. Surprising, however, are the seasonal temperature relationships between the Great Basin hybrids (Fig. 4, line 1) and the present-day hybrid belt (line 2) particularly in regard to minimal temperatures throughout the year and to summer maxima. While the average elevation for the three stations supplying data for the present-day hybrid belt is slightly more than 500 feet above that for the two stations in the Salt Lake area representing the altitudinal extremes of the northern relictual hybrids, the average minimal temperature for the former is 3.6 degrees lower than for the latter. The minimal average temperature for the year at New Harmony is 3.6 degrees lower (see Table I) than that of the Dry Canyon station, which has the same elevation but is 280 miles farther north. Also, minimum temperatures for the three station average of the area of present-day hybridization (line 2) are consistently lower throughout the year (except for the period from December 26 to February 19) than temperatures of the northern Great Basin hybrid stations (line 1). In regard to average maximum temperatures, only line 1, Figure 4, shows that the summer is significantly warmer for the northern Great Basin hybrids than for the northernmost present-day hybrids.

The greatest temperature difference between these two hybrid zones, however, and one which appears to us to be the most significant, is seen in the late fall, winter, and early spring regimens. For 16 weeks (October 3-February 19) the northernmost recent hybrid locations (line 2) consistently maintain an average daytime temperature of about 10 degrees higher than the northern relictual hybrids of the Salt Lake area (line 1). The strong suggestion, therefore, derived from a study of Tables I and II and Figure 4 is that the temperature factor or factors responsible for the disappearance of *Q. turbinella* from the Great Basin with the onset of the present climate was not colder minimal temperatures at any time of the year, nor colder maximal temperatures during late spring, summer, or early fall, but a significant drop in total warmth during a protracted period beginning in late fall and extending into early spring.

In order to test this hypothesis, further aspect analyses of the temperature data given in Table I, as well as of the continuous temperature charts,

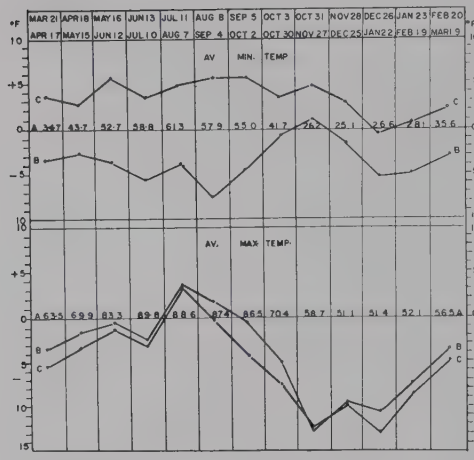

FIG. 5. Graph showing thermal departures of Dry Canyon (line C) and Oquirrh No. 1 (line B) from New Harmony (line A).

seem desirable. Figure 5 is designed to show graphically the thermal departures of Dry Canyon (C) and Oquirrh No. 1 (B) from the maximum and minimum temperatures prevailing at New Harmony (A) for each of the 13 four-week periods throughout the year. The New Harmony temperatures are indicated numerically for each period on a straight base line, and those of Dry Canyon and Oquirrh No. 1 are represented by variable graphic departures from the specific temperatures given for New Harmony.

The minimum temperature graphs for the two Great Basin stations show wide divergence from the New Harmony temperatures. Except for one period (December 26-January 22), the temperature of Dry Canyon is consistently higher than that at New Harmony, and temperature at Oquirrh No. 1, except for one period (October 31-November 27) is lower. The year's average for the Dry Canyon stations is 3.6 degrees above that for New Harmony, and the year's average for Oquirrh No. 1 is 3.6 degrees below. Since *Q. turbinella,* a major component of the oak complex at New Harmony, is absent from Dry Canyon, where minimal temperatures are higher than at New Harmony, as well as from Oquirrh No. 1 where they are lower, the minimal temperature average as an important factor in the extinction of the live oak parent in recent times within the Great Basin can probably be ruled out.

In contrast to the great disparity in average minimal temperatures between Dry Canyon and Oquirrh No. 1 as compared to New Harmony (as seen in Fig. 5), the graphs showing maximal temperature relationships emphasize similarities rather than differences. While the maximal temperatures at the Oquirrh station are consistently higher than those at Dry Canyon almost throughout the year, there is no great difference at any time. Both stations are similar also in a gradual decline of maximal temperatures below those of New Harmony for ten months between September and July. From late fall to early spring the average maximal temperatures at New Harmony exceed those at Dry Canyon and Oquirrh No. 1 by more than 10 degrees.

Because both Figures 4 and 5 clearly indicate that high winter daytime temperatures constitute a major difference of climate separating the northernmost populations of *Q. turbinella* (line 3, and A) from the northern Great Basin hybrids (line 1, and B, C), Figure 6 was designed to present

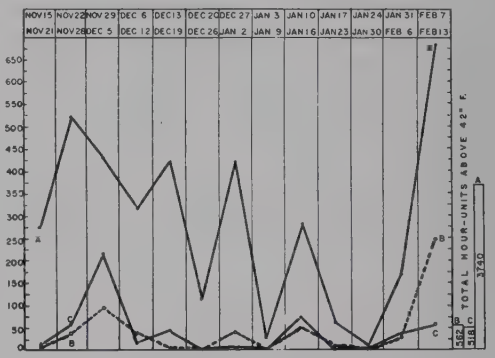

FIG. 6. Graph showing "effective growing temperatures" (hour-units per week above 42° F.) for 13 coldest weeks in winter of 1956-57.
A: New Harmony, B: Oquirrh No. 1, C: Dry Canyon.

this difference quantitatively. The time period selected extends from November 15, 1956, to February 13, 1957, involving 13 weekly records during the coldest part of the year.

Admittedly we have no specific data regarding the cardinal temperature characteristics of any physiological processes such as respiration or photosynthesis for the various oaks involved in this study. Lacking such data a minimum figure of 42 ° F. was selected for measuring "effective" temperatures. In other words, the lines of the graph in Figure 6 merely express the number of hour-units per week exceeding 42° F.

The results are striking, whatever the significance of 42° F. may be in relation to the functioning of *Q. turbinella.* Throughout these 13 weeks of winter, the "effective" temperatures available to the latter species at New Harmony compared to those available in the Salt Lake area

bear a ratio of 7 to 1, or a daily average of 41 to 6 hour-units.

The winter of 1956-57 must be considered generally mild and open for both the eastern Great Basin region and for that portion of Utah and Arizona lying directly south, with which this study is concerned. It is interesting, however, that the coldest temperature recorded for any of the northern Great Basin hybrid stations or the northernmost recent hybrid stations was at New Harmony. The following are the lowest temperatures recorded for these several stations: Dry Canyon 11° F., Oquirrh No. 1 5°, New Harmony 0°, Glendale 4°, and Mt. Trumbull 4°.

It has long been recognized that a sudden drop of temperature to an extreme low for a short period is far less important in plant distribution than a prolonged extreme of the same degree. Shreve (1911) found that the giant cactus, *Carnegiea gigantea,* is limited in distribution to areas where continuous periods of freezing temperatures are not prolonged beyond 18 hours.

Table III was therefore constructed to show the number and length of periods exceeding 24 hours with temperatures continuously below 32° F. for the various oak stations. Again the results appear significant. No such period was recorded for Pintura, where *Q. turbinella* alone is found. For the three stations harboring both parents and hybrids (Glendale, New Harmony, and Mt. Trumbull), the number of these periods did not exceed 3, and their duration not more than 42 hours. For the two northern hybrid stations in the Great Basin, 8 such periods were recorded with durations as great as 140 hours. Data were not available for the Gambel oak belt except for the lower altitudinal limits of its range. These show as many as 14 periods with durations as much as 150 hours continuously below freezing.

The failure of *Q. turbinella* to persist in central and northern Utah at the present time may be related in some way to its evergreen habit. Certainly evergreen shrub species are more common southward through the chaparral and pinyon-juniper woodland areas of Arizona, where *Q. turbinella* reaches its optimal development, than in central and northern Utah at comparable altitudes. At higher elevations in Utah, of course, where winter snow lends a protective cover, such evergreen shrubs as *Ceanothus velutinus, Arctostaphlyos patula* and *Pachystima myrsinites* comprise a conspicuous feature of the forest undercover and sometimes appear in open spaces as dominants. Except for *Arctostaphylos patula* in the Wasatch range, these shrubs are important constituents of the mountain flora all along the ranges comprising the eastern confines of the Great Basin. All of them are found in abundance

TABLE III. Number and length of periods in hours exceeding 24 with temperatures continuously below 32° F. for all stations. The number of figures in each "box" indicates the number of such periods

Stations	NOVEMBER			DECEMBER 1956			JANUARY 1957			FEBRUARY			Oak Species
	1-10	11-20	21-30	1-10	11-20	21-31	1-10	11-20	21-31	1-10	11-20	21-28	
Pintura	—	—	—	—	—	—	—	—	—	—	—	—	Q. turbinella
Mt. Trumbull	—	32	—	42	—	—	—	—	—	—	—	—	Both Parents & Hybrids
Glendale	—	36	—	42	32	—	—	—	—	—	—	—	Both Parents & Hybrids
New Harmony	—	—	39	—	—	39	—	—	—	—	—	—	Both Parents & Hybrids
Dry Canyon	—	39	65	52	32	74	—	—	42 32 130	—	—	—	Relictual Hybrids
Oquirrh No. 1	—	39	68	—	—	40	40	—	140	—	—	—	Relictual Hybrids
Oquirrh No. 2	—	62	73	117	—	69 80 42	70 48 68	84	60 40 150	69	—	—	Q. gambelii
Emigration Canyon	—	39	69	92	—	134	40 42	48	115 42 95	—	—	—	Q. gambelii
Kanarraville	—	63	—	62	—	39	—	—	112	—	—	—	Q. gambelii

TABLE IV. Comparison of monthly mean maximum and minimum temperatures (F.) at Salt Lake Airport (Alt. 4220 ft.) with Dry Canyon station (Alt. 5280 ft.) 1956-57

Month	1956										1957	
	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
S. L. Airport Max. 1956-57	54.9	62.7	73.6	85.6	92.7	88.8	84.5	65.9	45.9	40.0	35.5	50.1
Dry Canyon Max. 1956-57	52.0	59.9	72.6	84.3	93.0	88.1	82.7	62.9	46.5	41.0	36.9	49.6
Dry Canyon Departure	− 2.9	− 2.8	− 1.0	− 1.3	+ 0.3	− 0.7	− 1.8	− 3.0	+ 0.6	+ 1.0	+ 1.4	− 0.5
S. L. Airport Min. 1956-57	29.8	37.1	47.2	53.5	60.0	56.6	49.4	38.3	22.6	20.0	16.4	30.4
Dry Canyon Min. 1956-57	33.0	41.0	52.0	60.8	66.1	64.1	61.1	45.0	30.8	27.9	24.0	35.2
Dry Canyon Departure	+ 3.2	+ 3.9	+ 4.8	+ 7.3	+ 6.1	+ 7.5	+11.7	+ 6.7	+ 8.2	+ 7.9	+ 7.6	+ 4.8

above the *Q. turbinella* belt of southern Utah, along with *Garrya flavescens,* which is only rarely encountered in the Great Basin.

Thus the prevalence of broadleaf-evergreen shrubs in the present climatic environment of *Q. turbinella* and the near absence of this growth form in the altitudinal zone of the Great Basin formerly occupied by this live oak are undoubtedly correlated with (a) the great difference in total hour-units of "effective" temperatures during the winter between the two areas (Fig. 6) and (b) the difference in number and duration of periods of sub-freezing temperatures (Table III).

It is interesting to note that the hybrid is intermediate in leaf persistence between the two parental species. In November its leaves gradually become brown and dry, but persist throughout the winter. It is probably intermediate in winter hardiness, also, having undoubtedly inherited some degree of cold resistance from its Gambel oak parent. This has been sufficient, however, to enable it to survive the onslaught of the present climate of the Great Basin in areas where *Q. turbinella* has been eliminated.

Finally, the temperature data presented in this paper suggest some necessary revision of concepts regarding the details of Altithermal seasonal temperatures. Antevs' (1955) temperature curve for the Neothermal gives an estimated 3.8° F.[2] maximal July mean temperature differential between our present climate and the Altithermal. However, the July mean at present is no higher at New Harmony than at Oquirrh No. 1 and considerably lower than at the Dry Canyon station. The one important suggestion for post-pluvial climatology provided by our data is this: the significant change in temperature from the Altithermal to Medithermal climates was not a general decrease in temperature throughout the year, but a distinct decrease in total warmth during the winter months.

[2] It is interesting that the data presented in this paper show a mean annual temperature, at present, precisely 3.8° F. colder than the Altithermal—if Oquirrh No. 1 is compared with New Harmony (Table 1). This is perhaps only a coincidence, however, for rather different results are obtained if the comparison is made between the *averages* of the two northern hybrid stations and the three southern hybrid stations (Glendale, New Harmony, and Mt. Trumbull).

Importance of Temperature Inversion on Oak Distribution in the Salt Lake Area

Attention has been called to the fact that the hybrids in the Great Basin are confined to a narrow altitudinal belt located near the base of the Wasatch escarpment and on the foothills of other mountain systems marking the eastern confines of pluvial Lake Bonneville. The average elevation of this belt is approximately 5400 feet and closely parallels the coinspicuous high water beach lines of the old lake some 200 feet lower. Below this Bonneville beach the hybrid oak seldom is encountered, although from the bottom of the Jordan Valley at the Great Salt Lake to the hybrid oak of either the Wasatch or Oquirrh Mountains is an altitudinal differential in excess of 1000 feet. Furthermore, although soil salinity of the valley is sufficient to have excluded oak here, Gambel oak flourishes in relative abundance on the well-watered and salt-free bench lands and steeper slopes over the more than 500 feet altitude that separates the valley floor from the Bonneville beach.

This phenomenon of the cool-loving species thriving at lower elevations than the warmth-requiring hybrid would seem a bit puzzling, since temperature generally decreases at the average rate of one degree F. for every 300 feet rise in altitude in this area. This remained a puzzling question until our temperature data began to reveal definite evidence of strong temperature inversion along the Wasatch front and to a lesser extent along the base of the Oquirrh Mountains.

Table IV, which compares the monthly mean maximum and minimum temperatures at the Airport with the Dry Canyon station shows that: (1) The daytime or maximum temperature at the Air-

port, 1060 feet lower than the Dry Canyon hybrid oak station, provided only one degree Fahrenheit monthly average above the Dry Canyon station, and that for 4 months of the year the temperature at Dry Canyon was higher. (2) The night-time or minimum temperatures at the Airport were significantly lower than those at Dry Canyon for all months of the year by a monthly average of 6.5 degrees. (3) Inversion is weakest during the spring months from February through May. September shows the greatest magnitude and March the least.

A synoptic study of the climatology of diurnal inversions of the Jordan Valley for the ten-month period beginning August, 1956, was carried out by Dickson (1957). He utilized surface and upper air data from the Salt Lake City Airport and surface data from the lower slopes of the Wasatch just east of Salt Lake City. His highest station was located at the mouth of Red Butte Canyon, about one-half mile south of and 160 feet lower than our Dry Canyon station. He determined that inversion conditions are "associated with calm, clear nights and relatively low humidities. Hence they are more frequent during anticyclonic conditions." It is under these conditions that the coldest temperatures occur. They insure that the extreme minima reached near the valley floors would not be realized along the sloping sides of the valleys at the elevation inhabited by the hybrid oak.

Dickson further showed that the inversions were somewhat deeper (1346 ft. av. for Dec. 1956) and more persistent in winter, though there is no indication that winter inversions are stronger than summer ones. The strongest inversion he reported amounted to 20° F., which occurred the evening of May 6, 1957. The strongest inversions at Dry Canyon were 18° F. recorded for three consecutive nights, September 17, 18, 19, 1956.

The Dry Canyon station was set up February 1, 1956 and discontinued March 21, 1957. The average minimum temperature for February, 1956 was 2.5° F. higher than at the Airport, but for February, 1957, the difference was twice that figure (4.8° F.). Thus it appears that the inversion characteristics for the same month vary from year to year as the storm patterns vary. Furthermore, a comparison of Dickson's data with the Dry Canyon station suggests that the magnitudes for the same inversion are not entirely constant at the same elevation along the Wasatch front.

These data strongly suggest that inversion phenomena are at least partly responsible for the peculiar altitudinal distribution of the hybrid oak in the Wasatch and Oquirrh Mountains. Similarly, inversion phenomena may well have "channelled," altitudinally, the northward migration of *Q. turbinella* along the mountains on the eastern fringes of the Great Basin during Altithermal times. The factors that govern the development of inland diurnal inversions must have been as operative then as now and perhaps with even greater effectiveness because of a different climatic regimen. The complete desiccation of lakes in Nevada and the complete melting of glaciers in the Rocky Mountains are strong presumptive evidence of both a drier and a warmer climate—facts that indicate greater predominance of anticyclonic conditions.

Correlation of Long-term Temperature Data from the U. S. Weather Bureau Records

In formulating the over-all plan for this study, it was realized that a statistical analysis of available long-term temperature data for the Great Basin and Colorado Drainage (for areas nearly contiguous to those of the 1956-57 stations) would be necessary in order to indicate the probable degree of reliability that a single year of temperature records might offer. It seemed desirable to ascertain the mean monthly maximum and minimum temperatures that characterize these areas, their standard deviations, and the departures of the 1956-57 temperatures from these long-term averages.

For such an analysis we were of course limited by the scarcity of U. S. Weather Bureau records. In southern Utah, St. George (alt. 2800 ft.), 25 miles southwest of the New Harmony station, and Cedar City (alt. 5834 ft.), 20 miles northeast of New Harmony, were selected for study. In the Great Basin, Salt Lake City Airport, located between the Dry Canyon and Oquirrh Mountain stations, seemed best suited for the purpose.

Table V which summarizes the results of these analyses, shows that: (1) The temperature characteristics of the year of this investigation (March 21, 1956-March 20, 1957) approximated the long-term averages. (2) At no station did more than one-third of the monthly departures exceed the standard deviation, and in only one instance did a departure exceed two times the standard deviation. (3) The general seasonal variations of temperature for all stations are similar, although, because of differences in altitude, latitude, and physiography, the three stations differ considerably in mean temperatures. (4) Significant monthly departures, such as a cool November, 1956, and a warm February, 1957, are similar for all stations.

TABLE V. Temperature comparisons of 1956-57 with long-term averages

Month	St. George, Utah								Cedar City, Utah								Salt Lake City, Utah							
	Maximum av. 50 years	Standard Deviation	Maximum 1956-57	Departure	Minimum av. 50 years	Standard Deviation	Minimum 1956-57	Departure	Maximum av. 50 years	Standard Deviation	Maximum 1956-57	Departure	Minimum av. 50 years	Standard Deviation	Minimum 1956-57	Departure	Maximum av. 50 years	Standard Deviation	Maximum 1956-57	Departure	Minimum av. 50 years	Standard Deviation	Minimum 1956-57	Departure
1956																								
March	68.7	4.0	72.2	+ 3.5	35.0	3.8	33.4	− 1.6	53.0	4.5	56.6	+ 3.6	27.4	3.8	23.6	− 3.8	50.7	4.3	54.9	+ 4.2	30.1	2.6	29.8	− 0.3
April	74.3	3.6	76.6	+ 2.3	40.8	6.7	45.0	+ 4.2	61.7	4.6	61.2	− 0.5	34.7	4.1	32.6	− 2.1	62.1	4.2	62.7	+ 0.6	37.8	3.0	37.1	− 0.7
May	84.4	6.0	88.5	+ 4.1	49.0	5.4	53.7	+ 4.7	71.2	4.6	73.9	+ 2.7	41.8	4.6	42.8	+ 1.0	71.7	4.4	73.6	+ 1.9	45.2	3.4	47.2	+ 2.0
June	94.8	3.5	99.6	+ 4.8	59.1	4.1	61.2	+ 2.1	81.1	3.3	86.8	+ 5.7	48.8	4.3	50.2	+ 1.4	81.5	3.8	85.6	+ 4.1	52.2	2.2	53.5	+ 1.3
July	100.4	3.7	100.9	+ 0.5	64.6	3.4	68.3	+ 3.7	87.1	2.8	88.2	+ 1.1	57.1	4.3	57.2	+ 0.1	92.0	2.0	92.7	+ 0.7	61.2	1.6	60.0	− 1.2
Aug	98.0	4.6	98.9	+ 0.9	62.8	3.7	67.2	+ 4.4	84.5	2.6	86.2	+ 1.7	56.6	3.7	53.8	− 2.8	89.7	1.9	88.8	− 0.9	60.0	1.8	56.6	− 3.4
Sept.	91 7	1.2	97.7	+ 6.0	52.2	9.0	58.2	+ 6.0	77.4	3.1	83.0	+ 5.6	47.5	4.7	49.2	+ 1.7	79.7	3.1	84.5	+ 4.8	49.8	2.2	49	+ 0.4
Oct	79.0	4.1	80.9	+ 1.9	41.2	4.2	44.7	+ 3.5	65.2	4.0	67.3	+ 2.1	36.7	4.6	35.1	− 1.6	66.1	4.0	65.9	− 0.2	39.8	2.3	38.3	− 1.5
Nov	64.6	3.2	63.7	− 0.9	30.4	3.5	26.3	− 4.1	53.2	4.6	51.5	− 1.7	26.5	4.1	14.9	−11.6	49.1	5.0	45.9	− 3.2	27.7	3.9	22.6	− 5.1
Dec	53.4	5.0	57.0	+ 3.6	24.4	5.6	23.8	− 0.6	39.7	4.6	45.2	+ 5.5	19.0	4.6	14.6	− 4.4	39.8	4.6	40.0	+ 0.2	22.3	5.6	20.0	− 2.3
1957																								
Jan	52.8	5.1	52.3	− 0.5	24.5	5.2	31.5	+ 7.0	41.2	5.0	38.5	− 2.7	17.9	5.7	15.8	− 2.1	35.8	6.2	35.5	− 0.3	17.4	7.6	16.4	− 1.0
Feb	58.9	5.2	65.7	+ 6.8	29.7	5.0	39.9	+10.2	45.0	4.8	50.7	+ 5.7	21.2	4.8	27.5	+ 6.3	40.7	7.7	50.1	+ 9.4	23.3	6.8	30.4	+ 7.1

These figures demonstrate quite unmistakably a general agreement between the long-term average and the period of this investigation, and show that the year was not an extraordinary one.

SUMMARY

1. Hybrids between *Quercus gambelii* and *Q. turbinella* have been found on the foothills of the Oquirrh and Wasatch Mountains in north-central Utah and at scattered localities on lower mountain slopes along the eastern boundary of Pluvial Lake Bonneville. *Quercus gambelii* is common through this region, but the present northern limits of *Q. turbinella* in southern Utah lie some 260 miles south of the most northerly hybrids. The obvious question posed by this situation is: At what period in past geologic time did the range of *Q. turbinella* occur this far north?

2. *Quercus turbinella* is an evergreen shrub of semi-arid chaparral or pinyon-juniper woodland in the Southwest, commonly occurring at elevations from 3500 to 6000 feet; *Q. gambelii* is a deciduous shrub or small tree, common at somewhat higher elevations in the ponderosa pine zone in the Rockies and mountains of the Southwest. The hybrids are, in general, intermediate in morphology and in length of leaf persistence. They commonly occur on south-facing slopes below the optimal range of Gambel oak, but where they occur at comparable altitudes, Gambel oak is more abundant on cooler, less-exposed slopes.

3. The available evidence suggests that some, if not most, of the hybrid clones are F1's; such clones may well be very old. Alternative hypotheses to account for their existence without the northward migration of *Q. turbinella* are discussed briefly, but are regarded as untenable.

4. Hybrids have also been found in southwestern Utah and northwestern Arizona in areas where the ranges of the parental species overlap at the present time. These hybrids differ in no important respect from, and present much the same range of forms as, the relictual northern hybrids in the Great Basin.

5. Evidence is considered which renders it improbable that *Q. turbinella,* or even the hardier *Q. gambelii,* could have persisted along the Wasatch during the period of Wisconsin glaciation. It is concluded that the postpluvial Altithermal period of Antevs, which lasted from about 7500 to about 4000 years ago, and was marked by a warmer and drier climate than at present, provided the necessary conditions for the northward migration of *Q. turbinella.* Then, in the subsequent Medithermal period, climatic conditions once again became sufficiently cool to have exterminated *Q. turbinella,* but not the hybrid.

6. Continuous temperature records were taken over a period of one year at eight stations in an attempt to gather data which would provide (1) some indication as to the thermal requirements of *Q. turbinella* and the hybrids, and (2) some basis for reconstructing important features of the climate of the Altithermal period. The data obtained suggest that the temperature factor(s) responsible for the disappearance of *Q. turbinella* from the Great Basin with the onset of the present climate was not a general decrease in temperature throughout the year nor colder winter minimal temperatures, but a significant drop in total warmth during a period from late fall to early spring. Evidence for this is seen in the facts that (1) the average daytime temperature during winter was about 10° F. higher at the areas of

present day hybridization than at those of the northern relictual hybrids, and (2) the periods exceeding 24 hours with temperatures continuously below 32° F. were fewer and of shorter duration in the former.

7. The average elevation of the relictual hybrids in the Great Basin is approximately 5400 feet, and they are seldom encountered very much below this. Gambel oak, however, flourishes in relative abundance down to levels more than 500 feet below this. This peculiar altitudinal distribution of the hybrids appears to be due to temperature inversions. Data are presented which demonstrate the existence of inversions along the Wasatch front and, to a lesser extent, on the Oquirrhs.

8. Comparison of temperature data for 1956-57 with long-term temperature averages from two localities in southern Utah (St. George and Cedar City) and one in northern Utah (Salt Lake City) shows a general agreement and also shows that 1956-57 was not an unsual year.

References

Antevs, Ernst. 1955. Geologic climatic dating in the west. American Antiquity **2:1:** 317-335.

———. 1948. Climatic changes and pre-white man. University of Utah Bull. **38:20:** 168-191.

———. 1952. Cenozoic climates of the Great Basin. Geologische Rundschau **40:** 94-108. Stuttgart.

Axelrod, D. I. 1939. A Miocene flora from the western border of the Mohave Desert. Carnegie Inst. Wash. Publ. **516.**

Bryan, Kirk and C. C. Albritton. 1943. Soil phenomena as evidence of climatic changes. American Journal of Science **241:** 469-490.

Cottam, W. P. and Rudy Drobnick. 1955. A new oak from Utah. Utah Academy Proceedings **32:** 33-34.

Deevey, E. S. and R. F. Flint. 1957. Postglacial hypsithermal interval. Science **125 (3240):** 182-184.

De Geer, Gerard. 1940. Geochronologia Suecica principles: Svenska Vetenskapsakademiens Handlingar **18:** 6. Stockholm.

Dickson, C. R. 1957. A synoptic climatology of diurnal inversions in the Jordan Valley. Master's thesis, Univ. of Utah.

Douglass, A. E. 1940. Estimated ring chronology 150-1934 A.D. Tree-Ring Bull. **6:** 4: Tucson.

Eardley, A. J., Vasal Gvosdetsky and R. E. Marsell. 1957. Hydrology of Lake Bonneville and sediments. Bull. Geol. Soc. Amer. **68:** 1141-1202.

Gale, H. S. 1914. Salines in the Owens, Searles, and Panamint basins southeastern California. U. S. Geol. Survey Bull. **580.** L. Washington, D. C.

Gilbert, G. K. 1890. Lake Bonneville. U.S. Geol. Survey, Monograph **1.** Govt. Printing Office, Washington, D. C.

Gvosdetsky, Vasal and H. B. Hawkes. 1953. Reappraisal of the history of Lake Bonneville. Bull. No. **60,** Utah Engineering Exp. Sta., Univ. of Utah.

Hansen, H. P. 1947. Postglacial forest succession, climate and chronology in the Pacific Northwest. Trans. Amer. Phil. Soc. **37:** 1: Philadelphia.

Jennings, J. D. 1957. Danger Cave. Anthropological papers No. **27:** 328 pp. Univ. of Utah.

Libby, W. F. 1951. Radiocarbon dates II. Science **114:** 291-296.

Matthes, F. E. 1939. Report of the committee on glaciers. Amer. Geophys. Union Trans. **20:** 518-523. Washington.

McMillan, Calvin. 1957. Nature of the plant community. IV. Phenological variation within five woodland communities under controlled temperatures. Amer. Jour. Bot. **44:** 154-163.

Palmer, E. J. 1948. Hybrid oaks of North America. Jour. Arnold Arb. **29:** 1-48.

Pendleton, R. C. 1952. Some uses of radioactive isotopes in ecological research. Doctoral thesis, University of Utah, Salt Lake City.

Sears, P. B. 1948. Forest sequence and climatic change in northeastern North America since early Wisconsin time. Ecology **29:** 326-333.

Shreve, Forrest. 1911. The influence of temperature on the distribution of the giant cactus. Plant World **14:** 136-146.

Suess, H. E. 1956. Absolute chronology of the last glaciation. Science **123(3192):** 355-357.

Van Winkle, Walton. 1914. Quality of the surface waters of Oregon. U. S. Geol. Survey Water Supply Paper **363.** Washington, D. C.

Williams, J. S. 1956. Geomorphic effects of the Altithermal in northern Utah. Utah Academy Proceedings **33:** 13-25.

PHOTOSYNTHESIS BY AQUATIC COMMUNITIES IN NORTHWESTERN OHIO

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During the years of 1957-58 the Atomic Energy Commission subsidized a study of productivity of aquatic habitats in Northwestern Ohio. This subsidy made possible the employment of faculty and student research workers[1] to gather data from a variety of aquatic habitats. Carbon dioxide change, under completely natural conditions, was measured by determining pH values at approximately four-hour intervals and relating these to a differential titration curve (Verduin 1956a). The phytoplankton populations were measured by counting the organisms that settled on the bottom

[1] Miss E. Eloise Whitwer and Dr. E. S. Hamilton of the B.G.S.U. Biology Department, and Dr. A. G. McQuate of the Hiedelberg College (Tiffin, Ohio) Biology Department contributed to this study. Student assistants were: Mrs. B. M. Mallory, Miss Frances Piasecki, Gerald Levy, David L. Drake, and Martha Havlick. (Contract Number AT (11-1)-536.)

of a Stender dish filled to a depth of one centimeter. A few drops of a fixative, recommended by Dr. Wilhelm Rodhe (Institute of Limnology, University of Upsala, Sweden) containing 10g I_2, 20g KI, and 20 ml. of glacial acetic acid in 200 ml. of water, were added and the organisms allowed to settle for 24 hours before counting. Such a sample represents a concentration about ten times greater than would be obtained by direct counts in a Sedgwick-Rafter cell. The objectives are immersed in the Stender dish while counting. Water immersion objectives can be obtained for this purpose but it is our experience that ordinary objectives work satisfactorily under these conditions.

With a 20X ocular, magnifications of 880 can be obtained for purposes of identification. The references used for identification were Tiffany and Britton (1952), Prescott (1951), and Forest (1954). Our counts were usually made at 100X and/or 440X magnification, depending on the sizes of the major components of the community. Some counts were also made at 28X magnification, when large aggregates, or large organisms, which could be counted easily at this low magnification, were present. Ten fields were counted per sample, and cell dimensions of 10 individuals of each major component were measured to yield estimates of phytoplankton volume. It has long been known that samples taken at intervals of a few minutes from the same station frequently differ by a factor of two or more in their plankton population, although the certainty of the counting procedure is greater than 90 per cent. I will not try to cite all the workers who have observed this phenomenon. Moberg (1918) described it and Doty (1957) describes similar variations in C^{14} uptake by surface samples collected at three minute intervals from a station in the Pacific Ocean. It is obvious that the intensive study of a single sample will not improve the representativeness of that sample. It would be better to collect five separate samples and count five fields in each, than to count five hundred fields in a single sample. The data reported in this paper represent not less than seven samples from each habitat studied. Data will be presented showing the hourly photosynthetic yield per liter of water, per square meter of water and per microliter of phytoplankton. No correlations with light intensity are included in this report. Work was seldom carried out in densely cloudy or rainy weather, so the data represent slightly better than average light conditions because the darkest days are excluded.

An intensive study of a small water-filled quarry (average depth 3m) near the University will be described first. Daily sampling of algal abundance, one sample per day from each of three depths (0.1, 1, and 2 m), revealed that when a specific component of the population first appeared its rate of increase for a few days amounted to a doubling of the population in from 0.5 to 2 days. This increase was followed by several days of relatively stable population density during which reproduction was approximately balanced by rate of loss, and neither rate could be determined from the data. It is significant that rates of population increase as high as a doubling in one day occur under natural condtions. Ragotzkie (1957) reported similar high rates, and these are several times higher than the rates I observed in western Lake Erie (1952a) or those I calculated from Lund's (1950) diatom population curves from Lake Windermere.

From the data obtained in this study it was possible to classify the plankton communities according to their volumetrically dominant species.

TABLE I. Phytoplankton communities of Urschel's Quarry, Bowling Green, Ohio. The dominant species are listed with their time of dominance and range of plant volumes of the total community

Time Interval	Dominant Species	Total Plant Volume μL/L*
June 14-25.....	*Scenedesmus bijuga* — *Oocystis parva*	2- 4
June 25-July 16..	*Gleocystis gigas* — *Glenodinium quadridens*	2- 8
July 16-24.....	*Glenodinium quadridens* — *Ceratium hirudinelia* — *Anabaena planktonica* — *Pandorina morum*	4-30
July 25-August 23	*Aphanizomenon flos-aquae* — *Glenodinium quadridens* — *Anabaena planktonica* — *Pandorina morum*	11-40

* a μL=10^9 cubic microns=1 cubic mm

In Table I these are listed with the time interval of dominance and the volume range of the community during this interval. A striking feature of this table is the importance of flagellates in these communities. The species listed are described as common or abundant in taxonomic literature but taxonomic studies do not include estimation of volumetric dominance, and progress in ecological classification of phytoplankton communities awaits wider application of volumetric studies.

During the fall and winter months (October through March) the Urschel's Quarry communities were dominated by *Cryptomonas ovata* and

Chlamydomonas globosa. The densest populations of the year were observed under the ice in March, when plant volumes of 130 μL/L were measured. In April, after the ice disappeared, an *Asterionella formosa—Fragillaria crotonensis* community arose, which attained population densities of 17 μL/L, at the end of April, and disappeared about the third week of May.

The photosynthesis determinations in Urschel's Quarry included a study of pH change at three depths (0.1, 1, and 2 m). The data are summarized in Table II. The yields were computed

TABLE II. Photosynthetic rates in Urschel's Quarry. Rates per unit water volume and per unit plant volume are shown

Time Interval	Depth (m)	Plant Volume μL/L	CO_2 Absorbed	
			μmol/L/hr	μmol/μL/hr
June 25-July 16...	0.1	4.3	8.7	2.0
	1	3.9	4.0	1.0
	2	5.6	1.3	0.2
August 5-August 22	0.1	29	26	0.9
	1	23	18	0.8
	2	19	14	0.7

using the maximal yield observed during a four-hour interval, thus they do not represent average values for the entire day. This table shows that the relatively low phytoplankton crops of early summer yielded higher photosynthetic rates per μL of plant matter in surface samples than the denser crops observed in August. The maximum rates observed on individual days, however, were about 4 μmoles of CO_2 absorbed per μL/hr. Fantastically high rates, as reported by McQuate (1956) for Sandusky Bay, were not encountered. McQuate suggested that small organisms were escaping detection in the Sedgwick-Rafter cell at 100X magnification. It seems likely that the method used in the present study, utilizing 440X magnification, insured detection of the small forms. It seems significant, however, that an inverse relationship is evident between population density and photosynthetic yield per unit of plant volume in the surface samples. McQuate's study also demonstrated such a relationship, and John C. Wright (private communication) has observed it in Canyon Ferry Reservoir, Montana. Wright's phytoplankton counts were made with an inverted microscope, thus also permitting high magnification study. Wright's maximal photosynthetic yields are approximately 4μmol/μL/hr. Talling (1957) observed similar maxima in African waters. Both the maximal, and the average photosynthetic yields, observed in studies of this type, where phytoplankton populations in natural density are studied, are 2-3 times higher than the yields I obtained (Verduin, 1956a) when using diatom populations concentrated with a bolting cloth net and studied at densities of about 100 μL/L. Under such conditions the average yield at optimal light intensity is 0.5 μmol/μL/hr. Studies similar to the one described here are being conducted in western Lake Erie (supported by the National Science Foundation) and these show average photosynthetic yields of 1.6 μmol/μL/hr., and maxima of 5. The low yields exhibited by bolting cloth concentrates may represent the natural rate of the larger forms so collected, but it is also possible that the unnaturally high population density had in inhibiting influence on the photosynthetic rate.

Table II shows that maximal CO_2 change occurred in the surface waters. The inhibition of photosynthesis, usually observed in surface bottles when clear and black bottles are used, apparently is not so significant a phenomenon that it can be detected in the 0.1 m samples under completely natural conditions. It seems likely that vertical turbulence makes the PH changes observed in the 0.1 m samples approximately representative of the zone of optimal light. In the study of CO_2 changes under completely natural conditions two obvious sources of error should be considered: (1) the absorption of carbon dioxide from the air, and (2) the evolution of carbon dioxide by community respiration. Because Urschel's Quarry water usually contains some carbonate both of these would tend to make the CO_2 change observed during a four hour interval under these conditions smaller than the true CO_2 absorption. The maximal rate of CO_2 transfer across an air-water boundary in well-stirred water is about 2.3×10^{-3} cm/sec (Bohr, 1899). This would represent a gain of only 1 μmol/L/hr if all the entering CO_2 were confined to the upper meter of water. This computation is of considerable interest to ecologists. It is made as follows: the CO_2 concentration of normal air is 13 μmol/L, and water in equilibrium with normal air will have a similar CO_2 content, i.e. the partition coefficient is close to unity. It is convenient, and theoretically defensible, to regard Bohr's rate coefficient as an index of the resistance encountered in boundary layers within the water, and to assume that the actual water-air interface reaches equilibrium in negligible time. The CO_2 concentration drop across these boundary layers then has a value of 13×10^{-3} μmol/cm³. This is

multiplied by the rate coefficient, 2.3×10^{-3}; by 10^4 (cm^2/m^2) by 3600 (sec/hr) to yield 1100 μmol CO_2 gain/m^3, assuming all the CO_2 entering remained in the upper m^3. To facilitate comparison with CO_2 changes produced by photosynthesis this CO_2 gain is expressed as 1 μmol/L/hr, which is about 12 per cent of the 8.7 μmol/L/hr in the upper meter during the June-July period of table 2, and is only 4% of the 26 μmol/L/hr in the upper meter during the August period. Because this computation assumes a degree of turbulence rarely attained in nature, I infer that the average daily CO_2 exchange between air and water is probably less than 1% of the CO_2 changes within the water.

But the CO_2 evolved by community respiration is more significant. I have shown (1956a) that the respiration rate of concentrated algal populations averaged one-eighth of the optical photosynthetic rate. And the daily pH records show that nocturnal PH decrease is equal to the diurnal pH increase, indicating that community respiration replaces the CO_2 absorbed by photosynthesis. It seems likely, therefore, that total photosynthesis under optimal light, may be considerably in excess of the values in Table II. It is significant that the values in Table II, even when uncorrected for respiration, are similar to the values exhibited by vigorous laboratory cultures of Chlorella (Verduin, 1952b, Table I).

During the winter months the flagellate community exhibited the characteristics presented in Table III. The photosynthetic yields per hour and

TABLE III. Average CO_2 absorption by a flagellate community (Chlamydomonas-Cryptomonas) in Urschel's Quarry in winter

Phytoplankton Volume μL/L	CO_2 ABSORPTION	
	μmol/L/hr	μmol/μL/hr
27 (1-135)	16 (0-33)	1.4 (0.3-6.3)

The values in parentheses represent the range observed. This community flourished under an ice cover in water temperatures of 0-3°C.

per unit of phytoplankton crop were similar to those observed in mid-summer, and the density of photoplankton crops was as high as the densest crops observed in July and August. The midday light intensity at 0.5 m averaged 1 milliampere on the Weston photometer, which is approximately equivalent to 250 f.c., or about one-fortieth of full sunlight at midday in summer. This community seems to have been well adapted for efficient energy utilization in dim light and low temperatures. This community also displayed an inverse correlation between population density and photosynthetic rate per μL of plant matter. The high yield of 6.3 μmol/μL/hr was associated with a phytoplankton crop of 11 μL/L. Crop densities of the order of 100 μL/L consistently showed yields of less than 0.5 μmol/μL/hr.

The phytoplankton studies associated with this project required the determination of average volumes of the major components. The taxonomic literature provides ranges of cell dimensions but I have found few published values of average volumes for the major components of natural communities. Table IV presents values for the organisms encountered frequently in Urschel's Quarry during the summer of 1957. These determinations were made by Mrs. B. M. Mallory, who completed a Master's thesis on the ecology of algae during the year preceding her employment on this project.

TABLE IV. Average volume of organisms encountered frequently in Urschel's Quarry during summer of 1957

Organism	Volume (μ^3)
Fragilaria crotonensis	870
Pandorina morum (colony)	11,360
Glenodinium quadridens	9,500
Ceratium hirudinella	120,000
Trachelomonas volvocina	1,840
Euglena minuta	620
Chlorochromonas minuta	310
Dinobryon divergens	800
Gleocystis gigas	940
Scenedesmus bijuga (large)	85
Scenedesmus bijuga (small)	52
Scenedesmus quadricauda	260
Tetrahedron minimum	300
Ankistrodesmus falcatus	85
Palme a mucosa	100
Sphaerocystis shroeteri (large)	103
Sphaerocystis shroeteri (small)	17
Westella inearis	86
Coelastrum cambricum	74
Oocystis parva	320

The wide variation in volumes of different organisms emphasizes the importance of determining volumes instead of reporting populations as "numbers of cells per liter." The smallest organism in Table IV (*Shaerocystis shroederi,* 17 μ^3) is 7000 times smaller than the largest (*Ceratium hirundinella,* 120,000 μ^3), but if one were reporting these as cells per liter they would receive equal weight. For this reason, a roughly approximate estimate of volume is vastly superior to a highly accurate determination of number of cells per liter. Attention to cell dimensions also reveals interesting growth relationships. During a two-week period (June 14-July 1) *Scenedesmus bijuga* fell clearly into two size classes, but the small form was not observed during the first week. On June

22, when the small form first appeared, 75 per cent of the population was in the small form and by June 25 the large form had disappeared altogether. These observations suggest that the large form gave rise to the small form, and the transition was made so rapidly that only one or two generation times were required to complete it.

The data presented above were limited to the study of Urschel's Quarry. In addition to these studies a survey was made of several additional aquatic habitats to determine the range of yields encountered. The data appear in Table V.

TABLE V. Summary of productivity determinations, summer, 1957

Location	Euphotic zone depth meters	Av Phytoplankton L/L	μMOLES CO_2 ABSORBED		
			L/hr	m^2/hr x 10^{-3}	μL/hr
Urschel's Quarry	2	10	16	20	1.6
Powell's Pond	0.5	..	18	6	...
Sandusky River	0.5	1	5	1	4.0
Gooding's Pond	0.9	48	13	8	0.3
Miller's Quarry	8	4	1	5	0.8
NOBA Pond	1	8	11	8	2.2
Western Lake Erie (Verduin, Unpubl.)	5	6	10	32	2.3
Portage River	0.3	..	24	4	...
Steidtman S. Pond (L)	0.4	..	25	7	...
Steidtman S. Pond (s)	0.4	..	24	6	...
Maumee River	0.3	..	17	3	...
Sandusky Bay (McQuate, 1956)	0.7	10	15	7	0.8

These data reveal a narrow range of hourly yields per liter of water (mostly 10-25). The low yields in Sandusky River were associated with low phtytoplankton crops and high turbidities. The low yields in Miller's Quarry were associated with frequent cases of apparent CO_2 evolution (pH decline) during morning hours. This was the only habitat exhibiting this phenomenon frequently. The western Lake Erie data show the highest yields per unit area. It seems likely that the turbulence created by the seiches provides conditions which support exceptionally high productivity per unit area. In computing the yield per unit area the yield per liter of surface water was multiplied by 0.65 (Verduin, 1956b) to obtain the average yield in the euphotic zone and this product was multiplied by the euphotic zone depth to yield photosynthetic rate per square meter. Such a computation contains two questionable assumptions: (i) that the pH rise in surface samples represents CO_2 change in optimal light and (ii) that photosynthesis below one per cent of surface light is negligible. The yields per square meter in Table V are similar to the yields I computed (Verduin, 1956b) from the data of Manning and Juday (1941) and of Pennak (1949). Note, however, that Table II shows hourly yields per μL of phytoplankton 2-3 times higher than the yields in Table I of my 1956b paper, which represented a summary of the work of five authors. In that paper I stated that the yield per unit phytoplankton was the least reliable factor in the estimates of photosynthetic yield in lakes. The data presented here suggest that the yield per unit phytoplankton may be as high as 4 μmol/μL/hr in populations entering their exponential growth phase, and that the densest phytoplankton crops encountered under natural conditions show yields ten times lower than this. The average yields obtained from numerous random samples of natural populations will, of course, represent a composite of the variety of physiological and environmental conditions reflected by this range of photosynthetic yields.

Whenever one attempts to correlate metabolic rates under natural conditions with the environmental factors which seem most likely to exert important influences (nutrient concentration, temperature, light supply, etc.) one obtains a wide scatter similar, when presented graphically, to the pattern from a sawed-off shotgun (Verduin, 1954, Fig 2, and 1956a, Fig. 5). Correlation coefficients usually are less than 0.5, and frequently prove to be of slight statistical significance. Ryther (1958) reports data (his Fig. 2) which show that the oxygen production per unit chlorophyll *a* in marine phytoplankton is so variable that the highest yields observed are about ten times as high as the lowest yields. He states that experimental error may contribute considerably to the scatter, but this seems unlikely. The certainty of chlorophyll and oxygen determinations is not likely to be less than fifty per cent, so it is difficult to envisage a scatter, in which the extremes differ by an order of magnitude, as being importantly influenced by a fifty per cent error. I believe Ryther's data, and the data in the present report, as well as the other shotgun scatters one encounters in the literature, indicate that natural populations are indeed so variable that single determinations routinely deviate from the mean of several determinations by a factor of two, and the extremes encountered in thirty or more samples are likely to deviate from the mean by a factor of three. This variability does not make the mean value computed from several determinations any less valuable, or reliable, but recognition of the variability as a genuine phenomenon, and not an artifact of experimental error, permits one to place confidence in the extremes which may at times provide more

significant information than the mean. In this connection it is revealing to note that Ryther found a wider scatter in yields measured with the C^{14} method than in the oxygen production (Winkler) method, although the C^{14} method is about 1000 times more sensitive than the Winkler determination.

The wide variability in natural communities has two important implications, (i) it necesssitates the study of several samples to provide a reliable estimate of the population mean and (ii) it makes intensive study of individual samples unprofitable. For example, a phytoplankton count in which one strives for 95 per cent certainty is several times more tedious than one in which one strives for 75 per cent certainty. Yet, if the error is random, the mean of several samples counted with a certainty of 75 per cent will provide an excellent estimate of the population mean because random errors tend to cancel out when averaged. I believe that one of the major barriers to volumetric determination of plankton populations is a mistaken evaluation of the amount of work involved, which in turn is derived from the assumption that a certainty of 95 per cent must be achieved for individual samples.

The data in Table V formed a basis for our decision to study Urschel's Quarry intensively, because it is one of the highly productive waters discovered in the survey and it is on University property, thus providing control over its use and easy accessibility from our laboratory. The unusual results obtained from Miller's Quarry, however, indicate that an intensive study of it might yield information of fundamental importance to aquatic ecology, and we hope to include such a study in future plans.

There is no evidence in Table V that the streams studied show higher photosynthetic yields than less turbulent waters. Both the Maumee and the Sandusky Rivers, however, carry a heavy load of fine silt, as is evident from the restricted depth of their euphotic zones. It seems certain that light penetration severely limits photosynthesis in these rivers.

The results reported here show that the method I described for measuring photosynthesis under completely natural condtions (Verduin, 1956a) is sufficiently sensitive to yield reliable estimates in most fresh-water habitats. The daily pH changes, in the least productive habitats encountered, are about 0.1 pH units, a difference which can be measured with a certainty of 70 per cent using a Beckman Model G. Moreover, the fact that CO_2 changes of 10 μmol/L/hr are common indicates that photosynthetic yields under completely natural conditions can be measured simply by titrating 500 ml samples collected at 4 hour intervals, with 0.02N NaOH or H_2SO_4 (as appropriate), to the phenolphthalein end-point, and converting the observed values to μmoles of CO_2. The change usually encountered in a 4 hour interval would represent 1 ml of reagent and such a measurement can be made, under field conditions, with an accuracy of 90 per cent. Frances Piasecki, an undergraduate student employed on this project, tested this method on two aquatic habitats near Toledo during the summer of 1958 and obtained values similar to those presented in Table V above. When employing this method it is advisable to use an aerated reference sample (Verduin 1959) which has a CO_2 content in equilibrium with the atmosphere.

SUMMARY

A study of photosynthetic rates under natural conditions, using pH change as a measure of CO_2 change, revealed rates of 1-25 μmol of CO_2 absorbed per liter of water per hour, 1-32 m mol/m^2/hr and 0.3-6.3 μmol/μL of plant matter/hr. The average rates were 2-3 times higher than those reported in previous publications. The rates under natural conditions were distinctly higher than those obtained with a community enclosed in a bottle. The highest yields per μL were associated with relatively sparse populations (10 μL/L), the lowest with dense populations (100 μL/L).

REFERENCES

Bohr, Ch. 1899. Definition und methode zur Bestimmung der Invasions—und Evasionscoefficienten bei der Auflösung von Gasen in Flussigkeiten. Werthe der genannten Constanten sowie der Absorptionscoefficienten der Kohlensäure bei Auflösung in Wasser und in Chlornatriumlösungen. Ann. d. Phys. u. Chem. **68**: 500-525.

Doty, M. S. 1957. Current status of carbon-fourteen method of assaying productivity of the ocean. Mimeographed report to AEC on contract AT-(04-3)-15.

Forest, H. S. 1954. Handbook of Algae. Knoxville: Univ. of Tennessee Press.

Lund, J. W. G. 1950. Studies on *Asterionella formosa* Hass. II. Nutrient depletion and the spring maximum. Jour. Ecology **38**: 1-35.

Manning, W. M. and R. E. Juday. 1941. The chlorophyll content and productivity of some lakes in northeastern Wisconsin. Trans. Wisconsin Acad. **33**: 363-393.

McQuate, A. G. 1956. Photosynthesis and respiration of the phytoplankton in Sandusky Bay. Ecology **37**: 834-839.

Moberg, E. G. 1918. Variation in the horizontal distribution of plankton in Devil's Lake, North Dakota. Trans. Amer. Microsc. Soc. **37**: 239-265.

Pennak, R. W. 1949. Annual limnological cycles in some Colorado reservoir lakes. Ecological Monog. **19**: 233-267.

Prescott, G. W. 1951. Algae of the western Great Lakes area. Bloomfield Hills, Mich.: Cranbrook Inst. of Science.

Ragotzkie, L. A. and L. R. Pomeroy. 1957. Life history of a dinoflagellate bloom. Limnol. and Oceanogr. **2**: 62-69.

Ryther, J. and C. S. Yentsch. 1958. Primary production of continental shelf waters off New York. Limnol. and Oceanogr. **3**: 327-335.

Talling, J. F. 1957. Diurnal changes of stratification and photosynthesis in some tropical African waters. Proc. Roy. Soc., B, **147**: 57-83.

Tiffany, L. H. and M. E. Britton. 1952. The algae of Illinois. Univ. of Chicago Press.

Verduin, J. 1952a. Photosynthesis and growth rates of two diatom communities in western Lake Erie. Ecology **33**: 163-168.

———. 1952b. The volume-based photosynthetic rates of aquatic plants. Amer. Jour. Bot. **39**: 157-159.

———. 1954. Phyotoplankton and turbidity in western Lake Erie. Ecology **35**: 550-561.

———. 1956a. Energy fixation and utilization by natural communities in western Lake Erie. Ecology **37**: 40-49.

———. 1956b. Primary production in lakes. Limnol. and Oceanogr. **1**: 85-91.

———. 1959. Use of an aerated reference sample when measuring dissolved carbon dioxide. Ecology **40**: 322-323.

EFFECTS OF SEED IRRADIATION ON GERMINATION AND SEEDLING GROWTH OF CERTAIN DECIDUOUS TREES[1]

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The present investigation concerns the effects of acute doses of gamma rays on dormant and physiologically active seed of tree species native to the Eastern Deciduous Forest. Such effects could influence future forest communities as well as the results of tree breeding projects.

Seed of many tree species lie dormant in the soil over winter or for several years prior to germination. This seed could be subjected to irradiation over the entire period either from accumulated radioactive wastes or other sources of chronic radiation. Brief exposures to levels of radiation higher than those received from chronic radiation could also occur.

The radiosensitivity of crop and horticultural plants and seed has been more widely investigated than the radiosensitivity of native species. Much of this experimentation on crop plants has been done in search of mutants useful to man. The work in this field has been thoroughly reviewed by Smith (1958). The many radiation mutation research projects conducted at the Brookhaven National Laboratory have been outlined and reviewed by Shapiro and Sagawa (1957). The response of plants exposed to radiation varies from species to species whether the plants are exposed to acute or chronic radiation. These differences in plant radiosensitivity are governed by gentotype, chromosome number, moisture content, age of the seed irradiated, temperature of the seed before and after irradiation, oxygen content of the tissues during irradiation, chemical pretreatment of seed and length of the storage period following seed irradiation. Nilan (1956) has summarized the action of these many factors that alter the sensitiivty of a plant to X-rays and gamma rays.

In this study, high levels of gamma rays were used to determine whether seed irradiation could become an ecological problem.

Materials and Methods

Seed of 18 species (Table I) were collected as they ripened in Eastern Kentucky during the 1956-57 and 1957-58 seasons. Seed of each species were collected from a single tree or from a group of trees in the same area in an attempt to reduce the effects of genetic variability. The same trees were used as a seed source both seasons.

Seed of 14 of the 18 species have dormant embryos and were stratified in moist sand at 0-5° C. for the number of days listed (Table I). Seed of the 2 species with resistant seed coats (Table I) were soaked in concentrated sulfuric acid for thirty minutes to increase their permeability prior to stratification or planting.

During the 1956-57 season, seed of these 18 species were collected, irradiated, stratified, and planted at the close of the stratification period in an artificially illuminated laboratory, in a medium of equal parts of sand and sphagnum moss. The

[1] This investigation is based on work performed under Contract No. AT—(40-1)—2066 between the U. S. Atomic Energy Commission and Morehead State College, Morehead, Kentucky.

TABLE I. Dormancy, stratification period, and size of each sample used for species tested

Species	Type of dormancy[2]	Length of stratification in days[2]	Number of Seeds per Germination Test	
			Lab.	Field
Acer rubrum L.	dormant embryo	15	400	0
A. saccharinum L.	none	0	400	400
A. saccharum Marsh.	dormant embryo	90	200	200
Aesculus octandra Marsh.	dormant embryo	90	90	100
Carya ovata (Mill.) K. Koch	dormant embryo	120	100	150
Cercis canadensis L.	dormant embryo resistant seed coat	60	400	1,000
Fraxinus americana L.	dormant embryo	110	200	500
Juglans nigra L.	dormant embryo	120	100	100
Liquidambar styraciflua L.	dormant embryo	60	1,000	0
Nyssa sylvatica Marsh.	dormant embryo	80	300	0
Pinus rigida Mill.	dormant embryo	30	700	0
Platanus occidentalis L.	dormant embryo	50	800	0
Quercus alba L.	none	0	190	0
Q. prinus L.	none	0	150	60
Q. velutina Lamarck	dormant embryo	45	112	125
Robinia pseudoacacia L.	resistant seed coat	0	200	180
Ulmus fulva Michx.	dormant embryo	60	400	0
U. americana L.	dormant embryo	30	400	400

[2] Data from the U. S. Forest Service (1948).

temperature of the laboratory ranged from 20-27° C. during germination. Seed samples of 11 of these species were kept stratified until outdoor plantings could be made in the early spring.

During the 1957-58 season, seed of 9 of these species were collected for a second time. One seed sample of each was irradiated before stratification, and another sample from the same seed lot was irradiated immediately following stratification. Standard indoor and outdoor germination tests were run as outlined by the Forest Service of the United States Department of Agriculture (1948). Any seed that began to decay during stratification was discarded prior to planting. Germination failures of seed sound in appearance include both dormant and non-viable seed.

The seed samples were irradiated with 1,000r to 10,000r units of cobalt-60 gamma rays at the University of Tennessee—Atomic Energy Commission Research Station and 33,000r to 100,000r units of cobalt-60 gamma rays at the Oak Ridge National Laboratory.

Results and Discussion

Effects of Irradiation on Dormant Seed

Each of the species investigated had individual reactions to the various levels of irradiation tested. No two species of a given genus had the same reaction. Seed irradiation affected germination, seedling growth and survival (Tables II and III).

Germination in the laboratory following irradiation with 10,000r was reduced to zero for *Quercus alba* and to less than 65% of the control germination for *Quercus prinus, Q. velutina, Ulmus fulva, Pinus rigida, Carya ovata, Platanus occidentalis, Acer saccharinum,* and *Nyssa sylvatica.* Following dormant seed irradiation with 100,000r, *Fraxinus americana, Liquidambar styraciflua, Acer rubrum, Acer saccharum, Cercis canadensis, Robinia pseudoacacia, Ulmus americana,* and *Nyssa sylvatica* germinated in the laboratory. The hypocotyls of the latter six species did not elongate, their cotyledons began to enlarge at the soil surface and death occurred before the first true leaf

TABLE II. The effect of irradiation of dormant seed with 10,000r units*

Species	Percent Germination				Percent Survival			
	Laboratory		Field		Laboratory		Field	
	Control	Irrad.	Control	Irrad.	Control	Irrad.	Control	Irrad.
Acer saccharinum	85.2	48.0	72.5	29.2	44.2	3.5	70.5	1.0
A. saccharum	16.5	16.0	12.2	11.5	12.5	7.5	7.4	4.0
A. rubrum	73.2	69.0	....[3]	....	51.0	44.7	....	....
Aesculus octandra	94.3	82.0	88.0	69.0	84.0	82.0	82.0	54.0
Carya ovata	72.0	14.0	79.3	4.6	72.0	14.0	74.6	2.6
Cercis canadensis	86.2	85.0	46.2	6.1	70.5	67.0	15.8	1.8
Fraxinus americana	48.5	60.0	54.2	63.4	16.0	32.5	47.4	53.6
Juglans nigra	23.0	20.0	32.0	62.0	28.0	20.0	29.0	62.0
Liquidambar styraciflua	47.6	39.0	....	....	47.6	36.7	....	....
Nyssa sylvatica	17.0	11.0	....	....	15.6	4.3	....	....
Pinus rigida	41.3	6.0	....	....	23.5	0.0	....	....
Platanus occidentalis	23.3	13.2	....	....	13.2	8.0	....	....
Quercus alba	87.4	0.0	....	....	87.4	0.0	....	....
Q. prinus	73.7	1.2	43.2	0.0	73.7	1.2	25.0	0.0
Q. velutina	45.5	5.7	43.8	16.8	45.5	5.7	44.8	12.0
Robinia pseudoacacia	64.5	67.0	34.4	12.8	60.5	64.0	18.8	4.3
Ulmus fulva	50.0	1.7	....	....	8.5	0.0	....	....
U. americana	75.5	72.0	29.5	16.5	52.5	7.2	3.5	.75

* Gamma rays from cobalt-60 source.
[3] No field tests conducted.

TABLE III. Summary of effects of acute irradiation on dormant tree seed

Part affected	Nature of effect	Level of Irradiation	Species
Embryo			
A. General	Germination less than 20% of control.	10,000r	*Quercus alba* *Q. prinus* *Carya ovata* *Pinus rigida* *Ulmus fulva*
	Germination long delayed.	10,000r	*Carya ovata* *Quercus prinus*
B. Epicotyl	Roots develop extensively but the epicotyl never elongates.	10,000-100,000r	*Quercus alba* *Q. prinus*
		50,000-100,000r	*Quercus velutina* *Aesculus octandra*
C. Cotyledons	Enlargement is inhibited and seedlings die before the seed coat is shed.	10,000r	*Pinus rigida*
D. Hypocotyl	Elongation is inhibited. Cotyledons enlarge at the soil surface and all seedlings die before the first true leaf develops.	100,000r	*Acer rubrum* *A. saccharum* *Cercis canadensis* *Robinia pseudoacacia* *Ulmus americana* *Nyssa sylvatica*
Leaves	Puckering, fusion, dissection, and chlorotic sectors.	10,000r	*Acer rubrum* *A. saccharinum* *Aesculus octandra* *Cercis canadensis* *Carya ovata* *Juglans nigra*
Stems			
A. Apical meristems	Terminal buds do not develop on many plants.	10,000r	*Aesculus octandra*
		5,000r	*Quercus alba*
B. Internodes	Permanent inhibition of elongation of the first 2 or 3 internodes.	10,000r	*Acer rubrum* *A. saccharinum* *A. saccharum* *Nyssa sylvatica* *Platanus occidentalis* *Cercis canadensis* *Quercus velutina* *Robinia pseudoacacia* *Ulmus americana*

developed. *Fraxinus americana* and *Liquidambar styraciflua* seed germinated, survived the first critical season, and the seedlings are continued to grow in the field. Seed of the other 10 species irradiated with 100,000r did not germinate in the laboratory.

Germination tests for 11 species were also conducted in the field (Table I). All species except *Quercus velutina* and *Juglans nigra* had lower germination in the field than in the laboratory following irradiation with 10,000r. *Quercus velutina* seeds have a short dormant period, but the seeds were kept stratified until weather conditions were favorable for outdoor plantings. Many of the seeds that had dead embryos began to rot before outdoor plantings could be made, and were discarded. Consequently, the indoor and outdoor plantings of *Quercus velutina* can not be compared, for the seed samples were not the same.

Juglans nigra seed irradiated with 10,000r also had higher germination in the field than in the laboratory. This variation could not be attributed to the length of the stratification period prior to the indoor planting, for the control germination in the field and the laboratory did not vary widely. Seed samples collected from the same trees the following year did not have the same high level of field germination. The low level of laboratory germination in 1957 may possibly be attributed to poor sampling.

Field plantings were observed daily and none of the seed irradiated with 100,000r even began to germinate as it did in the laboratory.

Field germination is lower than laboratory germination, but the amount of variation ranges from slight for some species to great for at least a few. Thus, laboratory tests can not be translated directly into what will occur in the field.

The composition of any plant community is dependent upon survival rather than germination alone. When survival is computed in relation to germination, the intensity of the radiation effects are minimized severely if high survival follows low germination. Percentage survival (Table II) throughout this study was computed from the number of seedlings surviving the first season in relation to the number of seeds planted. The lower percentage survival of the seedlings from irradiated seed than from the controls is related to the effects of irradiation indicated in Table III. Emergence may be great in some cases following seed irradiation, but inhibition of the growth of the hypocotyl or cotyledons results in early death. The first true leaves of many seedings that survive the initial stages of germination have scattered chlorotic sectors and are puckered, dissected, or fused. If the seedlings survive this stage, the later leaves are not so affected. The mutant cells apparently die and the nonmutant cells seem to be the precursors of the new leaves. Seedling survival from this stage onward is about the same as that of the controls.

The level of irradiation that reduces survival to less than 30% relative to the control would decrease the number of seedlings to such an extent that it could have serious effects on the continuation of the species. This level of irradiation has been designated as being critical in this study.

The critical level of irradiation for dormant seed is less than 10,000r for the following species:

Acer saccharinum
Carya ovata
Cercis canadensis (field only)
Nyssa sylvatica
Pinus rigida
Quercus alba
Quercus prinus
Q. velutina
Robinia pseudoacacia (field only)
Ulmus americana
U. fulva

The critical level of irradiation for dormant seed is between 10,000r and 100,000r for the following species that had greater than 60% survival relative to the control at 10,000r and less than 30% at 100,000r:

Acer rubrum
A. saccharum
Aesculus octandra
Cercis canadensis (lab.)
Fraxinus americana
Juglans nigra
Liquidambar styraciflua
Platanus occidentalis
Robinia pseudoacacia (lab.)

Fraxinus americana and *Liquidambar styraciflua* were the only species that germinated and continued to grow following dormant seed irradiation with 100,000r.

Although seed germination and survival were lower in the field than in the laboratory, the critical range was the same for all except 2 species. Seed irradiation became critical between 10,000r and 100,000r in the laboratory and dropped to less than 10,000r in the field for *Cercis canadensis* and *Robinia pseudoacacia*. "Environmental changes are most conspicuous in the lowest portion of that layer of air in which life occurs. What happens to the seedling during this critical period of its life determines whether it shall live or die." (Wolfe, Wareham, Scofield 1949). Environmental variations occur more frequently and in greater intensity in the field than in the laboratory. Fewer seedlings from the irradiated seed survived these variations than the controls. *Cercis canadensis* and *Robinia pseudoacacia* seedlings reacted to these variations more intensely than the other species.

In an attempt to narrow the critical range of irradiation, seed samples of 9 species were collected again the following year (1957) and subjected to 5,000r, 10,000r, and 50,000r units of cobalt-60 gamma rays. *Quercus alba* and *Q. velutina* had such low germination and survival at 10,000r the first year, that samples were irradiated with 1,000r as well as 5,000r the second year. Seed samples of *Fraxinus americana* and *Liquidamber styraciflua* survived 100,000r the first year so they were retested at this level. The results of these tests are presented in Table IV.

TABLE IV. Critical range of irradiation measured in thousands of roentgen units of cobalt-60 gamma rays

Species	Seed Irradiation before Stratification		Seed Irradiation after Stratification	
	Lab.	Field	Lab.	Field
Quercus alba	1- 5	.....[4]	.....	.....
Q. velutina	5-10	5-10	.....	.....
Carya ovata	5-10	0- 5	0- 5	0- 5
Aesculus octandra	10-50	10-50	5-10[5]	5-10
Cercis canadensis	10-50	0-10	0- 5	0- 5
Fraxinus americana	Not valid	10-50	10-50	10-50
Juglans nigra	10-50	10-50	5-10[5]	5-10[5]
Liquidambar styraciflua	10-50	10-50	5-10	0- 5
Platanus occidentalis	10-50	Not valid	0- 5	Not valid

[4] No test conducted.
[5] Survival 40-49% of the control at 10,000r in these cases.

These laboratory tests for *Fraxinus americana* seed irradiated while dormant can not be considered as valid tests because the germination of the untreated sample as well as the irradiated samples was less than 5%. Apparently dormancy had not been broken before this planting was made, for germination in the field at a later date was high. Even the seeds subjected to 50,000r and 100,000r while dormant germinated in the field. These field seedlings did not survive the first true leaf stage, but the laboratory seedings from the seed irradiated with 100,000r did survive in 1957. These seedlings have been transplated to the field where they are continuing to grow.

Dormant seed of *Liquidambar styraciflua* irradiated with 50,000r and 100,000r did not yield any surviving seedlings in 1958. A few seedlings from the seed irradiated with 100,000r did survive in 1957 and after a year's growth in the field are slightly shorter but equally vigorous as the controls. The failure this year may have been the effect of an unidentified fungus that invaded the 50,000r and 100,000r seed samples during stratification rather than an irradiation effect.

The critical level of irradiation is lower than 50,000r for all species. Not a single seed irradiated with 50,000r gave rise to a seedling that survived the first true leaf stage in 1958. The critical range was narrowed from between 10,000r and 100,000r to between 10,000r and 50,000r for *Aesculus octandra, Fraxinus americana, Juglans nigra, Liquidambar stryraciflua, Plantanus occidentalis,* and *Cercis canadensis,* from between 0r and 10,000r to between 5,000r and 10,000r for *Quercus velutina* and *Carya ovata,* from between 0r and 10,000r to between 1,000r and 5,000r for *Quercus alba.*

TABLE V. Summary of effects of seed irradiation before and after stratification

Species	Effects of seed irradiation before stratification.	Effects of seed irradiation after stratification.
Aesculus octandra	1. Variation in height Control 9.9 in. ave. 5,000r 8.2 in. ave. 10,000r 5.4 in. ave. Number of plants with terminal buds. Control 100.0% 5,000r 40.0% 10,000r 10.0%	1. Variation in height Control 9.6 in. ave. 5,000r 6.4 in. ave. 10,000r 1.9 in. ave. Number of plants with terminal buds. Control 100.0% 5,000r 19.0% 10,000r 4.3%
Carya ovata	Germination low and long delayed.	Germination lower and longer delayed.
Cercis canadensis	Cotyledons enlarge at the soil surface when irradiated with 50,000r. Growth rate at 5,000r and 10,000r about the same as control.	Cotyledons enlarge at soil surace when irradiated with 5,000r and 10,000r. No germination at 50,000r. Growth rate at 5,000r and 10,000r much slower than control.
Juglans nigra	Rate of elongation same for control, 5,000r, and 10,000r. Some leaves dissected and fused at 10,000r.	Rate of elongation at 10,000r 1/5 that of the control. All leaves at 10,000r have many chlorotic areas and are severely dissected and fused.
Liquidambar styraciflua	Germination at 5,000r and 10,000r high in relation to control. Low germination and survival at 100,000r.	Germination and survival very low at 10,000r and 0 at 50,000r.
Platanus occidentalis	Rate of stem elongation and leaf enlargement at 5,000r and 10,000r not as rapid as control.	Germination and survival very low at 5,000r and 10,000r.

Comparison of Effects of Irradiation on Dormant and Physiologically Active Seed

The physiological status of these seeds was thought to be one of the principal factors affecting their radiosensitivity, because *Quercus alba,* which has no dormant period, is more sensitive than dormant species to irradiation. Seed of 7 species were irradiated before and following stratification to test this hypothesis.

The seed radiosensitivity of 6 of these 7 species is greatly increased as the physiological activity increases. Much lower levels of gamma irradiation are thus critical, once dormancy is broken (Table IV). Morphological effects are also more pronounced and occur at lower levels when irradiation follows stratification (Table V).

The radiosensitivity of dormant and physiologically active seed varies from species to species. The levels of seed irradiation which are critical to germination and seedling survival are high in comparison with the levels critical to man. If seedlings from irradiated seed survive beyond the 3 or 4 true leaf stage, their continued survival is equal to that of the controls, but the rate of growth may vary. The field seedlings from the dormant seed irradiated with 10,000r units of gamma rays are now more than a year old. *Aesculus octandra, Acer saccharum, A. saccharinum, Carya ovata, Quercus prinus,* and *Q. velutina* seedlings grew more slowly than the controls. *Platanus occidentalis, Fraxinus americana, Robinia pseudoacacia,* and *Liquidamber styraciflua* seedlings grew at a rate equal to the controls, but *Juglans nigra* seedlings grew more rapidly than the controls in the field. Even though the growth rate of year-old seedlings from irradiated seed does compare favorably with that of the controls, there is a big difference in the initial survival of the seedlings in the 2 groups. Furthermore one year of successful growth for seedlings from irradiated seed does not necessarily mean that these seedlings will have as long a life span or be as reproductive as the controls. Some of these seedlings and corresponding

controls have been planted in permanent sites on campus so that such observation may be continued.

Seed irradiation is a tool that could be used in forest breeding projects, once the levels critical to survival are determined. The seedlings growing from the irradiated seed exhibit changes, but screening for desirable mutants will still be a big task. However, seed irradiation is a means of increasing the amount of variability at the disposal of the breeder.

Summary

Dormant seeds of 18 species native to the Eastern Deciduous Forest were irradiated with acute doses of cobalt-60 gamma rays. Seed irradiation affected germination, seedling growth, and survival of each species in an individual fashion. Survival of the seedlings from seed irradiated with 10,000r is less than 30% in relation to the control for one half of these species in the laboratory and for 7 out of 11 in the field. *Liquididambar styraciflua* and *Fraxinus americana* were the only 2 species that germinated and had any survivals following seed irradiation with 100,000r. The radiosensitivity of the seed of 7 species was tested during and following the dormant period. Critical levels of seed irradiation were found to be much lower after dormancy had been broken.

References

Forest Service, U. S. D. A. 1948. Woody-plant seed manual. Misc. Pub. No. **654.**

Nilan, R. A. 1956. Factors governing plant radiosensitivity. Conf. on Radioactive Isotopes in Agr. U. S. A. E. C., TID **7512**: 151-162.

Shapiro, S., and Y. Sagawa. 1957. The Brookhaven coperative program for radiation mutation research. Ninth Oak Ridge Regional Symp. **11-35.**

Smith, H. H. 1958. Radiation in the production of useful mutations. Bot. Rev. **24**: 1-24.

Wolfe, J. N., Wareham, R. T., and Scofield, H. T. 1949. Microclimates and macroclimate of Neotoma, a small valley in central Ohio. Ohio Biological Survey. Bulletin **41.**

AN ALPINE SNOWBANK ENVIRONMENT AND ITS EFFECTS ON VEGETATION, PLANT DEVELOPMENT, AND PRODUCTIVITY[1]

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Snow distribution in alpine environments is far from uniform because of the interaction of wind and topography. Snow may fall relatively evenly, but, throughout the winter, strong winds remove snow from exposed slopes and ridges and deposit it in great drifts in the lee of these ridges and in other protected places. Snow melt comes early on the windward slopes and ridge-tops because of the relatively thin snow cover. The drifts, however, melt back slowly, exposing the ground in a series of daily increments. Many drifts eventually disappear during the short alpine summer, but others, except in severe drought cycles, have a hard core of more or less permanent névé.

The rate of snow melt has a considerable effect on the distribution of plants not only above timberline but within forested areas as well. Many meadows within the subalpine coniferous forests are maintained by the suppression of tree seedlings and saplings by the heavy snow cover of forest-caused drifts and the consequent short growing season.

Within the alpine tundra, the micro-zonation of species and communities is largely a function of the depth and melt-rate of the snowbanks. The plants in the windy areas of shallow snow cover emerge early, mature early, and must usually tolerate some degree of drought. On the other hand, those plants deeply covered by snow must be able to complete at least a vegetative life cycle quickly, and even that cannot be accomplished every year. Yet they have the protection of the snow in critical periods of high wind and low temperature, and seldom experience drought.

While the general effects of alpine snowbanks on vegetation are known (see Gjaerevoll 1956), there are relatively few data on the relationships between the snowbank type of environment and the distribution and growth of the plants associated with it. It was to get such information that the present investigation was conducted during the

[1] Appreciative acknowledgment is made to the Duke University Research Council for aid in supporting the field work on this problem. It is a pleasure also to acknowledge the help of Gweneth Bliss and Dr. J. F. Reed during the field operations.

summers of 1954 and 1955. The locale was a semi-permanent snowbank on the north side of Sugar Loaf Peak at approximately 11,000 ft. (3,353 m.) (106° 19′ W, 41° 20′ N) in the Snowy Range of the Medicine Bow Mountains, about 40 miles west of Laramie, Wyoming. The snowbank forms each winter on a long rock scree with a north-facing slope of approximately 10-12° (Fig. 1). In June of each of the study years, the dimensions of the bank were approximately 100 m long and 35 m wide, with a maximum depth at this time of about 3 m. In June of 1957 and 1958, the bank was much larger and deeper. Snowfall was above normal for these latter years but about 25 per cent below normal during the two study years.

FIG. 1. The snowbank in early July, 1954. The view is to the north, looking downslope from the upper meadow.

METHODS

Environment.—The pattern and rate of snow melt was followed each week from June to August by marking the outline of the snowbank on the rocks with paint; a different color was used each week. These will be referred to as "time lines." Snow depth was measured with a wire probe, and photographs were taken twice a week to show the general pattern of snow melt and the development of the vegetation.

Two instrument stations were established to measure certain microenvironmental factors. One station was located near the upper end of the snowbank in late June of each summer. The second station was installed at the base of the snowbank. Each station consisted of a Bendix-Friez hygrothermograph placed on the ground and covered with a ventilated white wooden box. Temperature and relative humidity were recorded at approximately 5 cm above the soil surface. The relative humidity data were later converted to vapor pressure deficit (VPD).

At each weekly time line, a pair of Sixe's type maximum-minimum thermometers was installed, one thermometer at 30 cm above the soil surface and the other at 2 cm below the soil surface in 1954, and at the 5 cm air and 2 cm soil levels during the summer of 1955. A Bendix-Friez 3-cup totalizing anemometer was installed near the upper station with the cups 55 cm above the soil surface. A Moeller 3-pen distance recording thermograph was placed near the anemometer with the sensing units at the 5 cm air, soil surface, and 5 cm soil levels in 1954. In 1955, the sensitive units of this instrument were used to compare 2 cm soil temperatures at three successive time lines.

Mean weekly temperatures were derived from hourly means. The mean maximum and mean minimum temperatures were obtained from daily maxima and minima. All temperatures are reported in °F.

Spot solar radiation measurements in gr cal/cm^2/min were made with a General Electric radiation meter.

Soil moisture determinations were based on oven dry weights of duplicate samples taken once a week at each time line. Samples were taken 2 to 5 cm below the soil surface.

Soil samples for analysis were collected along the June 28 time line on the upper edge and the lower edge of the bank. All analyses are averages of duplicate samples of the 2 mm soil fraction. Mechanical analysis was made using the hydrometer method (Bouyoucos 1936). Soil pH was determined with a Beckman pH meter using a 1:1 soil-water dilution. Moisture equivalent was determined with a moisture equivalent centrifuge, and the 15 atmosphere soil moisture tension with a pressure membrane apparatus.

Vegetation.—The vegetation was analyzed by means of 2 dm x 5 dm quadrat samples. Three such samples were taken at each time line along

transects at both the upper and lower edges of the bank. The quadrat data provided density and cover values for each species. Relative density values and cover percentages were added together to give a combined density-cover index.

Weekly phenological notes on the principal species were made along the time lines. Where possible, phenological observations included start of growth, leaf expansion, flowering, set of seed, ripening of fruits and seeds, seed dispersal, and leaf coloration.

In 1954, plant growth was measured by obtaining weekly oven dry weight samples of 25 *Geum turbinatum*[2] plants clipped along each time line at both the upper and lower transects. In addition, the current year's growth of 25 *Salix cascadensis* twigs was clipped weekly along certain time lines of the upper transect. In 1955, weekly clippings of *Geum* were made as in the previous year. In addition, along each time line on both transects duplicate 4 dm^2 quadrat clippings of total live vegetation were made weekly to measure net plant productivity. All data are expressed as oven dry weights. All clip quadrats were taken where vegetational cover was 100 per cent. Productivity figures presented in Tables V and VI have, therefore, been adjusted to the average percentage of vegetational cover/$meter^2$ as indicated by the vegetational analysis at each location.

Results

Environment.—During both 1954 and 1955, the snowbank was approximately the same size (ca. 100 m x 35 m) when observations began in late June. However, the pattern and rate of melt differed somewhat each summer. The reasons for these year-to-year differences in melt-rate patterns lie not only in summer weather conditions but also in differences in winter snow deposition patterns which depend upon the force and direction of the wind and upon temperature and storm frequency. These factors determine the physical nature of the drifted snow and just where it will lie. The winter weather factors are those primarily responsible for variability in snowbank morphology, while the local topography sets the general snowbank pattern which appears year after year.

In both 1954 and 1955, the snowbank melted away in approximately two months after the first observations were made in June. By August 17, 1954, only a very small patch of snow was left in the rocky center of the depression, while by August 16, 1955, all of the snow was gone. The depression was completely snow-free for several weeks in late August and September of both these years.

In contrast, during the heavy snow year of 1957 the bank when visited on July 24 still covered most of the outer time lines of 1954 and 1955. Thus, over a month later in the growing season, the bank was slightly larger than in late June of the observational years. There was still considerable snow left in the basin on September 9, 1957. It is unfortunate that detailed studies were not made on the bank and its vegetation during the unusual year of 1957.

The rate of melt varied from one part of the bank to another and also from time to time depending upon weather conditions. It was faster in the rocky scree areas due to the more rapid heating and re-radiation from the rocks as compared to that of the wet turf soils. Naturally, the rate of retreat was faster on gentler slopes where the snow cover was thinner. Maximum outflow of meltwater occurred during the early afternoon and flow usually stopped completely during the latter part of the night.

Assuming a north-facing slope of about 11°, the noon angle of incidence of solar radiation at the snowbank is about 37° 30′ at the equinoxes and 61° 30′ at the summer solstice. In addition, almost daily afternoon cloudiness and frequent thundershowers also cut down on the insolation total.

The only measurements of solar radiation were spot readings with a radiation meter. These readings were taken between 9 and 11 A.M. on clear or partly cloudy days. The averages of 10 observations each were: 0.83 gm cal/cm^2/min received parallel to the slope along the upper transect, 1.18 gm cal on the level area at the base of the lower transect, 1.53 gm cal normal to the sun's rays, 0.49 gm cal reflected from the snow surface, and 0.17 gm cal reflected from vegetation.

Temperature was the most intensively measured environmental factor. Air temperatures recorded at the 5 cm level by the hygrothermographs averaged 3°F lower at the lower station (Table I). This is the result of drainage of air down over the continuous cold snow surface, especially at night. Night minima near the surface were frequently near freezing with daytime maxima usually between 55° and 65°. Diurnal temperature range was usually about 20°.

Data from the three levels recorded by the distance thermograph during the observation period of 1954 show that temperatures at −5 cm. averaged 48.2°, at the surface 50.0°, and at the +5 cm. level 50.4°. The low surface temperatures

[2] Nomenclature for vascular plants follows that of Harrington (1954).

TABLE I. Mean maximum, minimum, and weekly temperatures (°F) at various positions around the alpine snowbank in 1954 and 1955

Week ending	5cm. Air Temperature 1954						Distance Thermograph Temperatures								
	upper transect			lower transect			5 cm. air			Surface			−5 cm. soil		
	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
July 11	61.3	46.7	52.9	62.7	44.1	52.4									
July 18	63.7	50.3	54.6	61.6	45.6	52.0									
July 25	54.3	47.4	54.3	59.3	46.2	51.4	63.1	41.1	50.3	68.1	34.4	46.3	51.4	36.1	44.1
Aug. 1	64.1	48.0	55.3	60.4	44.7	51.4	67.1	43.6	54.0	76.0	41.4	54.1	60.0	42.1	50.3
Aug. 9	63.4	46.9	53.9	59.8	43.4	48.5	64.0	41.0	50.8	75.3	40.4	52.6	60.8	42.3	50.3
Aug. 15	58.5	45.1	50.5	56.0	43.0	47.8	57.3	39.8	46.5	67.3	40.9	47.2	57.5	42.3	47.9
	5 cm. Air Temperature 1955						Thermograph Temperatures −2 cm. Soil								
	upper transect			lower transect			June 21 line			June 28 line			July 5 line		
June 28	57.0	41.4	49.0	55.3	39.0	46.9	59.0	33.6	45.0	52.9	33.4	42.5	46.0	32.6	39.2
July 5	59.4	39.6	48.4	56.4	35.4	45.6	64.6	36.3	48.4	56.1	33.6	44.4	69.9	31.1	37.9
July 12	62.0	42.0	51.7	58.0	38.3	48.0	66.4	38.6	50.7	59.4	38.0	48.4	77.1	40.4	53.0
July 19	65.3	42.4	53.5	62.3	39.2	49.9	79.1	41.0	57.9	66.5	40.3	53.8	66.5	40.7	56.4
July 26	60.0	44.7	52.2	58.0	42.7	49.1	67.7	44.2	53.8	65.8	45.2	55.2	66.7	44.7	54.3

are attributed to the water-saturated soils. All of these temperatures, especially the surface ones, are lower than those recorded at similar levels on a nearby north-facing slope (Bliss 1956).

In 1955, the distance thermograph leads were placed at depths of 2 cm along the June 21, June 28, and near the July 5 time lines. The mean temperature values for five weeks for each of the time lines were, respectively, 51.1°, 48.9°, and 48.2°. The lowest mean and mean minimum temperatures were recorded at the July 5 line, the last to be uncovered, and consequently colder for the first two weeks (Table I).

Precipitation, while not measured at the snowbank, was recorded on the same slope at a distance of less than 100 meters. For the month of July, 2.1 inches (53 mm) were recorded in 1954, and 2.0 inches (51 mm) during July, 1955. Much of this precipitation resulted from convectional thundershowers occurring usually in early afternoon at frequent intervals. Dry periods lasting a week or more do occur when stable Pacific air dominates the area.

The continuous record of relative humidity at both stations provided vapor pressure deficit (VPD) data throughout the period of observations. Weekly means based on hourly determinations ranged from 0.33 cm to 0.67 cm at the lowest transect in 1954. In 1955 the range was 0.31 cm to 0.64 cm and 0.25 cm to 0.59 cm at the upper and lower transects respectively. The week of highest VPD values was that of July 5 to 11, 1955, which corresponded to a period of high temperature and wind, as well as low cloud cover and no precipitation. In 1955, VPD was 9 per cent higher at the upper station than at the lower station for the five week period. Vapor pressure deficit was always low at night and reached its maximum in late morning or early afternoon.

Wind during the summer was less important as a factor around the snowbank than on the surrounding ridges. On a weekly basis, wind speed averages ranged between 3.8 m.p.h. and 5.4 m.p.h. in 1954 and 4.1 m.p.h. to 7.3 m.p.h. in 1955. There are few cushion plants in the snowbank vegetation as opposed to those on windy ridges where this growth form is very important. In general, it can be said that the snowbank is there because of reduced winter wind speeds, and the same relative wind condition prevails during the summer.

The soils along both transects are quite similar, with the exception of the peaty soils in the wetter areas beyond the lower edge of the bank. The mineral soils are sandy loams derived from the weathering of the Sugar Loaf metaquartzite and the Lookout schist of pre-Cambrian age. They contain a considerable amount of organic matter (13.5% loss on ignition), and have a pH range of 4.7 to 4.9 in the rather well-developed A horizon which is 15 to 18 cm deep. Below the A horizon, there is a thin transition zone which immediately grades into the C horizon. The analyzed soils (from the June 28 time line) are quite similar in physical properties to those found at the nearby north-facing station of Bliss (1956).

Although no analyses were made on the soils along the other time lines, it was observed that the A horizon becomes thinner on later time lines with less incorporated organic matter, until toward

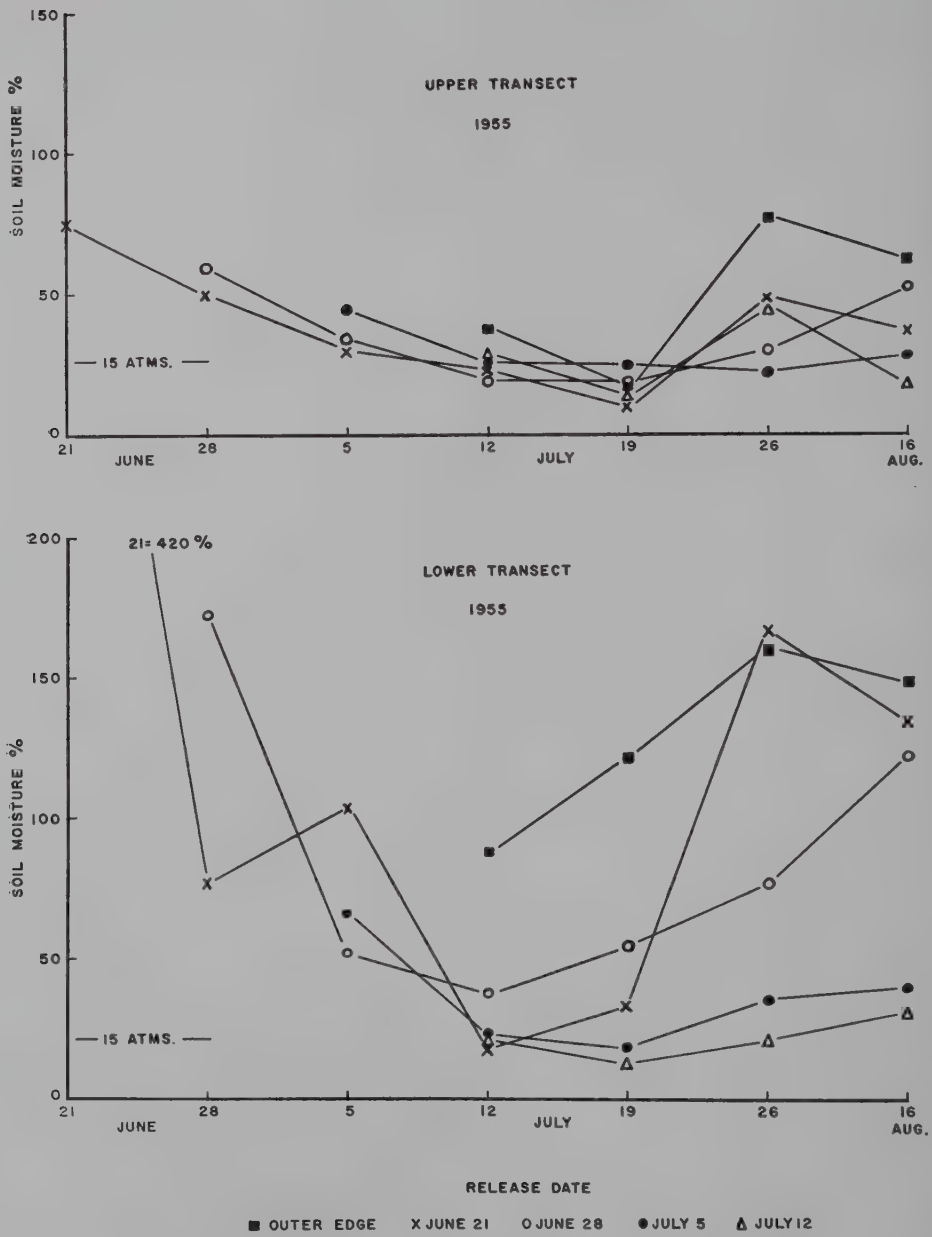

FIG. 2. Soil moisture percentages for the different time lines in 1955.

the center of the bank only the C horizon appears at the surface. These areas of later snow release (July 12 inward) support little vegetation and are snow free for only about a month or two at most.

Soil moisture in the snowbank area seldom showed tensions of more than 15 atmospheres, and then only for short periods of time (Fig. 2) The melting snow kept the lower transect quite moist until the end of the growing season. On

this transect, the lowest soil moisture values occurred toward the middle of the bank area, near the end of the season. The outer edge of the lower transect was always quite high in water content due to the effect of high organic matter on field capacity and actual retention and to the funneling of meltwater through this meadow. On the upper transect, there was some tendency for the outer, more exposed, locations to dry out to tensions above 15 atmospheres, but these periods were always cut short by thundershowers. Here, too, the higher organic matter content away from the middle of the bank was reflected in higher moisture contents later in the season on the earlier time lines as compared to those time lines exposed late where vegetation and organic matter are almost non-existent.

Vegetational composition.—The ridge top above the bank (15 m beyond the outer limits of the snowbank on June 21) is dominated by *Salix cascadensis, Geum turbinatum, Trifolium parryi, Artemisia scopulorum,* and *Carex drummondiana.* With the exception of the willow, which is a snowbank indicator, the community is quite similar to those found in other alpine meadows of the Medicine Bow wherever adequate soil has developed. Progressing toward the center of the bank, the number of species and degree of plant cover decreases while the percentage of bare soil and rock increases until the latter cover the entire surface (Table II). All of the species that dominate on the ridge or along the outer time lines are either absent or poorly represented in the area uncovered in July. *Carex elynoides, Deschampsia caespitosa,* and *Sibbaldia procumbens* dominate both above and at the base of the bank where the surface is released from snow after the end of June.

At the base of the bank where melt water provides more soil moisture, the wet meadow community (4 m. beyond the outer limit of the bank on

TABLE II. Vegetational analysis along the 1955 time lines at both upper and lower transects for the alpine snowbank. Data are combined density-cover percentages

Species	Upper Transect Time Lines						Lower Transect Time Lines					
	Ridge Top	June 21	June 28	July 5	July 12	July 19	Wet Meadow	June 21	June 28	July 5	July 12	July 19
Geum turbinatum	23.3	80.7	49.9	7.7	....	.....	32.8	11.1	35.1	0.8	11.5	....
Salix cascadensis	59.8	26.0	27.3	....	....	.....	....	7.9	24.0	42.0	....	.....
Festuca ovina var. *brachyphylla*	8.4	21.3	7.1	9.7	....	.....	....	6.2	2.7	3.0	....	.....
Arenaria obtusiloba	2.4	7.5	4.5	....	....	.....	....	5.5	8.7	6.8	5.1	.....
Trifolium parryi	19.3	5.1	....	....	....	.....	....	....	5.0	....	....	.....
Polygonum bistortoides	1.2	4.8	....	....	....	.....	2.8	3.4	4.3	....	....	.....
Chionophila jamesii	0.8	3.0	....	....	....	.....	....	....	1.4	....	....	.....
Artemisia scopulorum	16.9	....	1.3	....	....	.....	....	12.0	21.0	1.4	4.4	.....
Selaginella densa	4.7	....	2.9	....	....	.....	....	3.7	8.9	....	....	.....
grass, vegetative	1.8	....	2.2	....	3.2	.....	....	2.3	....	....	....	.....
Silene acaulis	2.0	....	0.7	....	....	.....	....	....	....	....	....	.....
Potentilla diversifolia	1.2	....	2.0	....	....	.....	4.1	13.1	7.1	....	....	.....
Carex drummondiana	14.5	....	....	....	....	.....	....	....	....	2.2	....	.....
Polygonum viviparum	9.0	....	....	....	....	.....	....	5.6	....	....	....	.....
Agrostis bakeri	4.7	....	....	....	....	.....	....	23.1	....	....	....	.....
Salix brachycarpa	2.4	....	....	....	....	.....	....	....	....	....	....	.....
Gentrana romanzovii	1.7	....	....	....	....	.....	....	....	....	....	....	.....
Erigeron sp.	1.2	....	....	....	....	.....	....	4.0	4.3	....	....	.....
Phlox caespitosa	1.2	....	....	....	....	.....	....	....	....	....	....	.....
Sedum rhodanthum	....	....	....	....	....	.....	83.3	2.7	5.7	....	....	.....
Carex sp.	....	....	....	....	....	.....	56.0	....	....	....	....	.....
Stellaria sp.	....	....	....	....	....	.....	6.6	....	....	....	....	.....
Sibbaldia procumbens	....	3.0	11.6	31.7	3.2	.....	....	29.2	6.0	33.5	24.3	.....
Carex elynoides	....	....	35.9	32.6	95.8	.....	....	17.5	5.3	34.8	27.3	.....
Antennaria umbrinella	....	2.4	....	....	....	.....	....	3.0	6.6	14.1	....	.....
Senecio cymbalaroides	....	....	....	....	....	.....	....	3.3	5.9	....	....	.....
Carex atrata	....	....	....	....	....	.....	....	1.8	6.7	....	....	.....
Erigeron simplex	....	....	....	....	....	.....	....	2.7	0.6	....	....	.....
Vaccinium scopulorum	....	....	....	....	....	.....	....	4.5	....	....	....	.....
Erigeron melanocephalus	....	....	1.3	....	....	.....	....	....	5.4	8.8	24.0	.....
Luzula spicata	....	3.2	....	....	....	.....	....	....	0.6	....	....	.....
Draba sp.	....	....	....	....	....	.....	....	....	....	4.5	4.4	.....
Gentiana tenella	0.5	....	....	....	....	.....	....	....	....	....	....	.....
Deschampsia caespitosa	....	....	6.6	53.3	30.5	.....	11.4	9.4	21.6	7.7	12.9	.....
% Moss Cover	1.7	....	1.7	7.3	10.0	.....	....	1.7	....	3.3	1.0	.....
% Bare Ground & Rock	21.4	43.0	50.0	57.7	57.3	100.0	2.0	27.2	28.7	37.1	75.1	100.0
Total Number of Species	20	10	13	5	4	0	7	21	20	12	8	0

June 21) is dominated by *Sedum rhodanthum, Carex* sp., and *Geum turbinatum*. Here, also, the number of species decreases toward the middle of the bank, while the percentage of bare ground and rock increases in areas of progressively later snow release. The number of species found at the July 12 release line was eight on the lower transect and only four on the upper. However, a greater percentage of the surface is occupied by plants at this time line on the upper transect.

The moss, *Polytrichum juniperinum* Hedw., provides increasingly more cover along the upper transect in areas uncovered later in the season. Nearly all of the moss cover was provided by this species. No lichens, except crustose forms on rocks, were observed in the snowbank area.

Plant development.—Many alpine plants begin growth at air and soil temperatures very near the freezing point of water. The species comprising the snowbank vegetation are especially well-adapted to this low temperature regime. *Geum turbinatum, Carex elynoides,* and *Deschampsia caespitosa* frequently grow under 1 to 5 cm of snow near the edge of the melting bank. *Deschampsia caespitosa* and *Carex elynoides* were observed to have started growth under 50 cm of snow in an area that did not become snow free for an additional four days. Temperatures at this location as recorded by the distance thermograph, ranged from 30° to 31° F at the soil-snow contact during this four-day period.

At any given time line, maximum flowering of most of the species occurred approximately three weeks after the intitiation of growth. Seed maturation and dispersal, in general, took about 7 to 8 weeks for most species in the present study.

The general pattern of phenological events at the various time lines is well-illustrated by *Geum turbinatum* in 1955 (Table III). There appeared to be slightly less time required for flowering in the plants released from snow at the later dates. However, observations were not made late enough in the season to observe whether there was any marked increased rate of seed maturation in these species. No significant differences between the upper and lower transects were observed in the developmental rate of plants of a given species at the same time line.

Primary productivity.—Clippings of both the total vegetation and of *Geum* alone show, in general, that maximum weight of the aerial portions of plants was reached somewhat before the end of the growing season (Tables IV to VI). This peak was attained usually in three to four weeks, except near the end of the growing season when there was a shortening of the time required for production of maximum plant biomass to about two weeks. Loss in shoot weight in August was due primarily to dispersal of seeds, withering of lower leaves, and translocation.

Weight of *Geum turbinatum* plants was always greater on the lower transect, and mature plant size and weight were lower at each successively later date there (Table IV). This pattern of reduced plant size was less evident on the upper transect, for total plant weight at maturity was frequently as great along July release time lines, as at those areas uncovered in late June.

The clip quadrat samples on the lower transect in 1955 show that total net plant production was also reduced at the lines released from snow at later dates (Table V). This is, in part, the result of a reduction in total plant cover, a shift in the species present, and the shorter growing season available for plant development. Along the upper transect, the standing crop in mid-August was greater on the July 12 line than on the June 21 line, although plant cover was considerably less on the inner line. This results partly from a shift in vegetation from low compact herbs at the earlier line to large scattered clumps of *Deschampsia caespitosa* and *Carex elynoides* at the latter. The maximum production on the June 21 line was reached in mid-July with a decline through August

TABLE III. Phenology of *Geum turbinatum* at the various release date lines for the upper transect (U) and the lower transect (L) at the alpine snowbank in 1955

Release Date	Date of Observation													
	June 21		June 28		July 5		July 12		July 19		July 26		Aug. 16	
	U	L	U	L	U	L	U	L	U	L	U	L	U	L
Outer Edge	V	V	B	V,B	B	B	B	F,B	B,F	B,F	F	B,F	S,C	S
June 21	I	I	V	V	V	V,B	B	B	B,F	B	B,F	B,F	F	F
June 28			I	I	V	V	B	B	B	B	B,F	B,F	F	F
July 5					I	I	V	V	B	B	B,F	B	F	F
July 12								I		V		B		F
July 19														

I initation of growth; V vegetative; B blooming; F fruits ripening; S seeds dispersing; C autumn coloration

TABLE IV. Oven dry weights in grams for 25 *Geum turbinatum* plants clipped weekly along the time lines at the upper transect (U) and the lower transect (L) for the alpine snowbank in 1954 and 1955

Release Date	Date of Clipping, 1954												No. weeks to reach maximum weight	
	July 11		July 18		July 25		Aug. 1		Aug. 9		Aug. 15			
	U	L	U	L	U	L	U	L	U	L	U	L	U	L
June 27	1.35	4.18	1.65	6.48	3.08	6.38	2.94	6.73	2.03	6.58	2.25	4.09	4	5
July 4	1.00	2.21	1.67	2.29	2.34	7.32	1.55	3.12	1.37	2.77	1.31	2.90	3	3
July 11	0.28	0.45	0.65	0.99	1.83	4.17	1.51	1.77	1.95	4.29	1.70	4.29	4	4
July 18				0.75		1.32		2.25		3.03		3.80		4

	Date of Clipping, 1955												No. wks. to reach max. wt.	
	June 21		June 28		July 5		July 12		July 19		July 26		Aug. 16			
															U	L
Outer Edge									5.66	14.03	6.01	15.62	5.75	23.69		
June 21	0.28	0.38	1.37	2.58	2.23	2.39	4.28	6.32	3.11	9.36	2.20	3.66	1.47	4.77	3	4
June 28			0.26	0.36	0.81	0.98	3.07	2.80	3.60	6.30	2.74	4.07	1.74	4.49	3	3
July 5					0.24	0.30	0.88	0.73	5.25	3.49	1.70	2.36	1.94	3.48	3	2
July 12								0.61		1.76		3.88		1.77		2

15 (Table V). It is believed that with a greater number of samples, this pattern of relatively higher total production might have been reduced at these areas released from snow later in the season.

Calculated net plant production per day is presented in Table VI. This shows reduced rates of production for the areas released at later dates on the lower transect. The average production per day for the season ending in mid-August, along the upper transect, however, was greatest on the July 12 release line and lowest on the June 21 line.

Maximum daily productivity is reached very soon after release from snow cover (within one to three weeks), then tapers off erratically until the end of the one to two month growing season. The high rates of shoot dry weight increase early in the season result from rapid translocation of carbohydrates upward from rhizomes and roots (Mooney 1958) and most of this gain, therefore, is really due to stored productivity from the previous year. During these first few days after snow-release, the sudden increase to full light intensity, the warming up of the soil and air, and the abundant soil moisture all combine with upward

TABLE V. Total plant standing crop, as oven-dry weights in grams/meter,^{2} of weekly clippings along the time lines around the snowbank in 1955

Release date	Clipping Date						
	June 21	June 28	July 5	July 12	July 19	July 26	Aug. 16
	Upper Transect						
June 21	5.0	19.7	34.2	57.8	52.0	38.5	36.2
June 28		3.4	19.5	26.8	27.0	19.4	34.0
July 5			6.1	18.5	9.5	19.5	35.5
July 12				23.2	11.6	38.8	40.0
	Lower Transect						
June 21	12.3	25.1	73.6	88.6	72.6	141.3	128.5
June 28		14.8	26.7	56.8	36.1	109.7	67.0
July 5			7.7	13.2	34.0	30.9	58.3
July 12				4.6	5.6	15.0	21.3

TABLE VI. Average daily plant productivity, as oven-dry weights in grams/meter^2/day of weekly clippings along the time lines around the snowbank in 1955. Figures are average daily dry weight increases per meter^2 from release date until clipping date

Release date	June 21	June 28	July 5	July 12	July 19	July 26	Aug. 16	No. of days from release until clipping
				Upper Transect				
June 21		2.8	2.5	2.8	1.9	1.0	0.6	56
June 28			2.8	1.9	1.3	0.9	0.7	49
July 5				2.6	0.7	1.4	0.8	43
July 12					1.7	2.8	1.1	36
				Lower Transect				
June 21		3.6	6.0	4.2	2.6	4.0	2.3	56
June 28			3.8	4.1	1.7	5.2	1.4	49
July 5				1.9	1.4	2.2	1.3	43
July 12					0.8	1.1	0.6	36

food translocation to cause rapid leaf expansion. Soon the plant is photosynthetically very active and daily rate of dry matter increase reaches its peak (Table VI). At this stage, for these plants, no environmental factor is now limiting. The soil and air have warmed up and the snow-melt water insures against early drought. Now, there is enough food being produced not only for flowering but to repay the underground carbohydrate reservoir (Mooney 1958).

The drop-off in daily productivity after this peak is primarily a function of reduced soil moisture; both soil and air temperatures are adequate and the scarcely shortened day-length in late July probably is not important in reducing carbohydrate synthesis. But along the older time-lines, the snow-melt soil moisture has now been lost through evapo-transpiration as soil and air temperatures have increased concomitantly with foliar surface increase. As long as the summer thundershowers come almost daily, soil moisture is maintained and productivity stays relatively high. Even a short drought, though, has marked effects on productivity. A comparison of Figure 2 and Table VI will show that the soil drought between July 12 and 19 resulted in a general drop in average productivity for the same week. Temperature was neither abnormally high nor low for the week, averaging 53.5° F for the upper transect and 49.9° for the lower. The rains between the 19th and 26th brought soil moisture to more favorable levels and productivity again increased. The week of June 28 to July 5, on the other hand, had the lowest mean temperature of any week during the growing season but daily productivity was high because soil moisture was not limiting.

Eventually, however, in August daily productivity drops off rapidly, probably as a result of a combination of short dry spells and lower temperatures. Dry weights of shoots tend to decrease because of this lessening production coupled with translocation to underground parts and loss of food in dispersing seeds and withering leaves.

The standing crop estimates throughout the summer on the lower transect show that total production is proportional to number of snow-free growing days. Thus, on August 16, standing crop was 128.5 gr/m^2 at the June 21 release line and only 21.3 gr/gm^2 at the July 12 release line. This reflects the great reduction in both plant ground cover and plant size with long-lying snow. In contrast, along the upper transect the standing crop remained about the same for the various release lines in the August 16 analysis (Table V). This high level of production in the areas released late in the season is believed to result from a shift in vegetational composition especially in growth form from low compact herbs in the areas released in June to large tussocks of grass and sedges in the areas released in mid-July.

At the end of the growing season, net production rates averaged 2.3 and 0.6 gr/m^2/day respectively at the lower and upper transects for the June 21 release line based on a 56 day growing season. On the July 12 release line, production rates at these same two transects were 0.6 for the lower and 1.1 gr/m^2/day for the upper based on a 36 day growing season.

Only a few data are available for comparing net shoot production in tundra ecosystems at the end of the growing season. In northern Alaska, an herbaceous community produced 0.9 gr/m^2/day based on a 70 day growing season (Bliss 1956). Alpine meadows in the same area as the present study averaged 1.2 gr/m^2/day for a 60 day growing season; the range was from 0.4 gr on a dry, windy ridge to 1.9 gr in a wet meadow and on a south-facing slope (Bliss 1956). Net production on Mt. Washington, New Hampshire averaged 2.1 gr/m^2/day based on a 60 day growing season (Bliss, unpublished data). These data include 1.2 gr for a heath-*Juncus* fell field, 2.1 gr for a heath-*Juncus* meadow, and 3.0 gr for a *Carex* meadow. At Abisko in Swedish Lappland, Pearsall and Newbould (1957) found that sub-arctic grass and sedge communities averaged 2.3. gr/m^2/day based on a 111 day growing season. Warren Wilson (1957) reported very low production figures of 0.05 gr/m^2/day for a *Salix* barren on Cornwallis Island in the High-Arctic. These production rates assume a 60 day growing season. It must be remembered that all of these rates are from ecosystems with only one turnover per year.

Conclusions

The data presented in this paper show that the slow summer melting of accumulated snow in alpine regions results in steep environmental gradients over a relatively small area. These environmental gradients produce similarly steep vegetational gradients, both floristically and from the standpoint of productivity. Many alpine species are restricted to snow-bank areas because of the protection provided there against winter desiccation and low temperatures, and summer drought. Growth and productivity are relatively high where release date is early or where meltwater flows daily. But long-lasting snowbanks shorten the growing season excessively, and thus cut down the productivity of the innermost plants in the

zonation. If snow release comes after late July in the central Rocky Mountains, primary productivity is almost nil, because only a few highly specialized alpine plants can survive under such a short and dry growing season.

Summary

1. A study was made of an alpine snowbank environment and its effect on vegetation, plant development, and net plant production in the Snowy Range of the Medicine Bow Mountains of Wyoming during the summers of 1954 and 1955.

2. Two microenvironmental stations were established at the snowbank; one above and the other at the base of the bank. Factors measured included: air and soil temperature, vapor pressure deficit, solar radiation, soil moisture, and wind. Time lines were painted each week marking the outer limits of the bank. Observations along these lines included: plant phenology, clippings of single plants and vegetation for productivity estimates, soil and air temperatures, and soil moisture.

3. Air and soil temperatures were quite low throughout the growing season although temperatures rose considerably following snow melt. Differences in temperature and vapor pressure deficit were small between the upper and lower end of the bank, and are believed to have little effect on vegetation differences. Soil moisture seems to be the most critical factor affecting vegetational differences above and below the bank. Wind velocity is less in the snowbank area than in the surrounding land.

4. Marked floristic vegetational differences were found along a gradient from the area released from snow in June to the areas uncovered in mid-July. These floristic differences are the result of differing tolerances of the species to drought and shortness of growing season. Accompanying the floristic changes in vegetation is the reduction in total plant cover, and an increase in large tussock-forming grasses and sedges. Soils are also poorly developed where the snow melts later than early July.

5. Plant growth begins in most species as soon as the snow melts, while a few start growth under a thin cover of snow. Growth and development is rapid, with many plants reaching full bloom in three weeks and producing ripe seed in 6 to 8 weeks. A slight speed-up was observed in phenology in those plants uncovered later in the growing season.

6. Clippings of vegetational quadrats and individual plants show that maximum standing crop was attained in about 3 to 4 weeks, followed by a slow decline to the end of the growing season. This same pattern was true for daily production. Along the lower transect, standing crop and daily production rates decreased with each succeeding time line; while on the upper transect, daily production rose at later time lines but did not result in an increase in standing crop.

7. End of the growing season net production rates ranged from 2.3 to 0.6 gr/m^2/day for the lower transect and from 0.6 to 1.1 gr/m^2/day for the upper transect. These values are from the outer to the inner time lines respectively. The production figures based on the entire growing season are comparable with those from other tundra ecosystems.

8. Productivity of snowbank vegetation is most closely related to high available soil moisture and relatively early release from snow. Late release dates provide too short a growing season for good plant and soil development. Soil drought is accentuated at these later release lines because of a relative lack of melt-water, relatively high evapotranspiration, and rocky soils low in humus.

References

Bliss, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. Ecological Monog. **26**: 303-337.

Bouyoucos, G. J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Sci. **42**: 225-229.

Gjaerevoll, O. 1956. The plant communities of the Scandinavian alpine snow-beds. K. Norske Videnskabers Selskabs Skrifter 1956 (1). Bruns Bokhandel, Trondheim. 405 pp.

Harrington, H. D. 1954. Manual of the plants of Colorado. Sage Books, Denver. 666 pp.

Mooney, H. A. 1958. Carbohydrate economy in relation to growth of certain alpine plants in Wyoming. M.A. thesis, Duke University. 52 pp.

Pearsall, W. H., and P. J. Newbould. 1957. Production ecology. IV. Standing crops of natural vegetation in the sub-Artic. Jour. Ecology **45**: 593-599.

Warren, Wilson J. 1957. Arctic plant growth. Advancement Science **13**: 383-388.

OBSERVATIONS ON THE BIOLOGY OF THE FAIRY SHRIMP, *EUBRANCHIPUS HOLMANI*

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INTRODUCTION

In the course of field studies dealing with the ecology and life history of the fairy shrimp, *Streptocephalus seali,* collections from certain localities were found to include individuals of a second species. Although differing in some respects from any published description the animals were finally assigned the name *Eubranchipus holmani,* a determination which was confirmed by Dr. Ralph W. Dexter. By reason of the special character of their habitat and the fact that *Eubranchipus* was limited in occurrence to the colder months of the year this form presented striking contrast to the much more ubiquitous *Streptocephalus.* Systematic observations made during the period 1951-1954 and continued in less regular fashion to the present are summarized in the following pages as a contribution to our knowledge of this little known fairy shrimp.

NOMENCLATURE

The anostracan branchipod currently known as *Eubranchipus holmani* (Ryder) has had a long and confused nomenclatorial history. First described by J. A. Ryder (1879) as *Chirocephalus holmani;* it has, in the ensuing three-quarters of a century, been reported some 10 or 12 times from widely scattered localities east of the Mississippi River under half a dozen different names.

Ryder's description was accompanied by 3 figures which, as Creaser (1930) has pointed out, are of little taxonomic value since they were inconsistent with the description and with each other. In one figure the clasping antennae were shown with 2 segments and in another with 3, although the text correctly described them as 2-segmented. Two long, fleshy, "proboscidiform appendages" were said to arise "from the bases of the claspers"; there was no mention as to whether they arose separately or from a single basal portion, although they were shown in the former condition in one of Ryder's sketches. The lack of specific information on this apparently minor anatomical detail has been a source of difficulty to many subsequent investigators. These appendages were shown as arising from the basal joints of the clasping antennae in one figure, and from the forehead above the first antennae in another. The extended length of the antennal appendages was specified to be 3 times that of the claspers, a proportion which was roughly substantiated by one figure.

Four years later, in 1883, Packard published his famous "Monograph of the Phyllopod Crustacea of North America." He stated that he had Ryder's types at hand, as well as additional specimens from New Jersey and Long Island. Packard repeated Ryder's statement regarding the relative lengths of antennal appendages and claspers, but he included a series of original measurements which would indicate that the former were actually less than twice as long as the claspers. He figured, in addition, a drawing of the head of an "old male" by Dr. C. F. Gissler in which the antennal appendages—here shown confluent at their bases—were no more than one-third longer than the claspers.

In 1910 Daday published his monographic revision of the Anostraca of the world. A European, Daday did not have access to the types or to any specimens of this form. His work was based on published descriptions which, as has been pointed out, were inadequate and inconsistent. Daday transferred Ryder's original form to the genus *Eubranchipus,* under the name *E. holmani.* The Long Island specimen, drawn by Gissler and figured in Packard's monograph, was assigned to another genus as *Branchinella gissleri* on the basis of the fact that Gissler's figure showed the proboscidiform appendage to be a bipartite structure arising from a single basal portion.

Apparently unaware of Daday's revision of the group, Fowler (1912) reported the collection of specimens from Chincoteague, Virginia under the name *Ino holmani.* He inspected Ryder's types, which had been deposited in the collections of the Philadelphia Academy, and reported them to be in fragmentary condition. Fowler's account of his specimens was paraphrased from the earlier descriptions of Ryder and Packard; his accompanying figure is not sufficiently clear with respect to the diagnostic characters of the head to enable one to say with certainty just what these characteristics were. The Virginia specimens are likewise no longer extant (Fowler, personal communication, 1952).

When Pearse (1918) prepared the section on Phyllopoda for Ward and Whipple's "Fresh-water

Biology" he followed Daday in listing both *Eubranchipus holmani* and *Branchinella gissleri,* suggesting that Packard had confused two species.

Creaser published his revision of the genus *Eubranchipus* in 1930. No specimens of this form, or forms, were then known to be extant in any collection. Creaser expressed the opinion that Packard, with the type specimens at hand, would not have confused species belonging to two different genera and accordingly united them provisionally as *Branchinella holmani.*

Mattox (1936) described a fairy shrimp collected at Tiptonville, Tennessee, under the name *Pristicephalus comptus.* He recognized the similarity of his specimens to Creaser's provisional *Branchinella holmani* (which Mattox suggested should probably be placed in the genus *Pristicephalus*), but assigned them a new name on the basis of several points of difference with Ryder's description. Chief among these were the proportions of the two segments of the clasping antennae, and the relative lengths of clasping antennae and antennal appendages. Mattox' paper remains the only really adequate description of the form, and his excellent figures have been used extensively by subsequent authors.

Linder (1941) tentatively accepted both *Pristicephalus comptus* Mattox (specimens of which he had not seen but which, on the basis of Mattox' figures, he suggested should possibly be transferred to the genus *Chirocephalopsis*), and *Eubranchipus holmani* (Ryder). He pointed out the difficulty of establishing clear and consistent generic distinctions within the Family Chirocephalidae and suggested (p. 282-283) that the forms belonging to the genera *Artemiopsis, Pristicephalus, Eubranchipus,* and *Chirocephalopsis* should perhaps be amalgamated under *Eubranchipus.*

Subsequent authors (Dexter and Kuehnle 1948, Pennak 1953, Dexter 1953) are inclined to the interpretation that only one species is involved, and that it should bear the name *Eubranchipus holmani* (Ryder). This interpretation is followed by the present investigator.

Distribution

Papers cited in the preceding section record the collection of *E. holmani* from the following states: New Jersey (type locality), New York, Connecticut, Virginia, Tennessee, and Ohio. Additional recorded collections include Louisiana (Moore 1951) and North Carolina (Daggy 1952). Dexter (1953, 1956) reviewed the geographic distribution of the North American fairy shrimps, reported additional collections of *E. holmani* from New York and Connecticut, and added new state records for Georgia and Maryland. I have not been able to substantiate a record for the state of Minnesota cited by Underwood (1886). It would appear that Underwood intended to attribute the Minnesota collection to Herrick (1885). Herrick's paper, however, did not specify the source of the specimens he identified as *Chirocephalus holmani* Ryder; nor did a later contribution (Herrick and Turner 1895) which included one of his previously published plates with the caption "Larvae of Chirocephalus."

Morphology

Disregarding minor structural differences, there appear to be two distinctive morphological forms of *E. holmani* represented in this series of collections. Like all Chirocephalidae, the species is characterized by a thoracic region of 11 segments and a 9-segmented abdomen (including 2 partially fused genital segments and a terminal telson which bears a pair of cercopods). Study of many hundreds of specimens collected from 4 Louisiana localities over a period of 19 years reveals that these adult males invariably possess a double row of dorsal spinous processes on the thorax and abdomen (Figure 1). The spines are well developed on the last 7 thoracic segments and the first 5 or 6 abdominal segments, being especially prominent in the mid-region of the body. Old females may show some traces of these spines but they are never conspicuous; I have never observed spines over .1 mm high in females, as contrasted to processes .5 mm or more in height in males.

Fig. 1. *Eubranchipus holmani* males. Upper: Louisiana specimen illustrating typical armature. Lower: Ohio specimen (coll., Dexter and Kuehnle) without armature.

Two collections totaling 14 specimens (4 males, 10 females) from Baker County, Georgia, have been examined. The males were all strongly armed; the females were unarmed or, in some cases, had a feeble armature more or less confined to the last 3 thoracic and the first 3 abdominal segments.

The armed males are thus to be found, as far as available collections indicate, only in the extreme southernmost part of the range of the species. I have studied specimens from Ohio, North Carolina, Connecticut, and Tennessee; no evidence of armature could be detected in any of the specimens examined. A small collection from Moulton in northern Alabama consisting of 4 mature males, two of which were quite dried, was also studied (U.S.N.M. 99396). The 2 undamaged specimens were without armature. Material from New York, New Jersey, and Virginia was not available for study; as a matter of fact the species has never been reported from the 2 latter states subsequent to its original collection. It seems unlikely, however, that such a striking feature as this armature would have escaped notice and mention by the earlier observers.

The presence of similar cuticular spines, as well as outgrowths having the form of warts, ridges, or bulges, has been described by Linder (1941) for several species of the genera *Branchinecta, Branchiopsyllus, Parartemia, Artemiopsis, Pristicephalus, Chirocephalopsis,* and *Chirocephalus.* In *Branchinecta paludosa,* for example, he notes and figures very similar paired dorsal spines on the 3rd-11th thoracic segments, inclusive, of adult females from certain localities. Collections of fully adult but unarmed females are cited from other localities, while a few collections of mixed armed and unarmed adult females are described. Linder regards the presence of unarmed females in the same population with armed forms as an example of neoteny; he considers the wide distribution of the armed form as evidence against the possibility of geographical races, but does not exclude the possibility entirely.

In the present case of *Eubranchipus holmani,* the occurrence of armed males only in extreme southern United States and the absence of any intergradations of form would lend weight to the thesis that we are dealing here with a geographic race or subspecies. It must be pointed out, however, that collections are few in number and scattered in origin and frequently consist of only a very small number of specimens. It would seem prudent, therefore, to defer the assignment of the armed form to a separate taxonomic category until more material from a greater number of localities becomes available for study.

Ecology

Habitat

Any discussion of *Eubranchipus* habitats in Louisiana must inevitably include mention of a second species of Anostraca, *Streptocephalus seali* Ryder. All known *E. holmani* habitats in the state are likewise *Streptocephalus* habitats, although the reverse is not the case, and mixed populations of the two species are not at all common.

S. seali is a large species, widely distributed throughout the state in ditches, pasture ponds, forest pools, and other types of seasonal habitats. It exhibits wide temperature tolerance, having been collected during every month of the year (Moore 1955).

In contrast, the smaller *E. holmani* has been collected only in southeastern Louisiana where it occurs in the heavily shaded, brown-water, cypress-sour-gum ponds scattered over the pine flats in eastern St. Tammany Parish. *E. holmani* is apparently a stenothermal species. It has been collected only in the winter months (late November to mid-March), and has not been taken at water temperatures exceeding 21°C. In this respect the form seems to be similar to other species of the genus *Eubranchipus,* all of which are cool-water dwellers.

Physico-chemical factors of the 4 known Louisiana habitats were determined on numerous occasions when populations of *Eubranchipus* were present. Methods employed have been described in a previous paper (Moore 1955). Water temperatures ranged from 9.0 to 20.5°C. The peaty soils and abundant leaf litter present in the basins were undoubtedly correlated with the low hydrogen ion concentrations noted, from pH 4.9 to pH 5.4, as well as with the high water color (140-360). The water of the ponds was invariably clear (less than 25 ppm turbidity), very low in total alkalinity (5.0-8.0 ppm), and usually exhibited high free carbon dioxide values (up to 20 ppm) and dissolved oxygen contents of less than saturation levels (1.0-4.5 ppm).

Season of occurrence

The deep, sheltered basins in which *Eubranchipus holmani* is known to occur flood only during periods of very heavy precipitation and ordinarily remain filled only during the cooler months when evaporation is minimal. Thus, winter rains in late November or December fill the basins and the pools may persist through April or May. Heavy summer precipitation may cause reflooding although this is infrequent and summer pools, when they occur, do not usually persist for long periods.

The 3-year history of a typical *Eubranchipus* habitat near Florenville, St. Tammany Parish, is illustrated in Figure 2. In March, 1951, an old population of *Eubranchipus* was observed which died off before the end of the month. The pond dried completely in June; reflooded temporarily in September at which time an abundant population

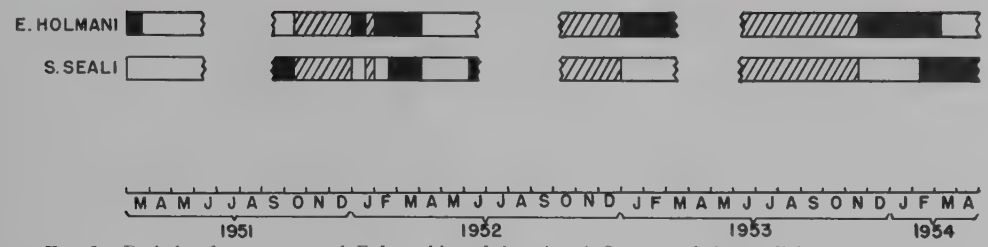

FIG. 2. Periods of occurrence of *Eubranchipus holmani* and *Streptocephalus sealí* in a cypress-sour-gum pond near Florenville, Louisiana. Black bar indicates fairy shrimp present; white bar, habitat flooded but no shrimp observed; shaded bar, habitat dry. A break indicates a period during which no field observations were made.

of *Streptocephalus* (but no *Eubranchipus*) appeared; then dried again, and remained in this condition until January, 1952.

Early January rains filled the basin to a depth of only a few inches and a hatch of *Eubranchipus* took place. The pool dried before these reached maturity, then refilled in late January and a second hatch of *Eubranchipus* occurred accompanied, a few weeks later, by a scanty population of *Streptocephalus*. Both species persisted until the end of March and died off. While the basin did not dry completely until late June, a slight additional fill in that month inundated previously dried-out borders and brought about a second small hatch of *Streptocephalus*.

The basin then remained dry until January, 1953, when winter rains flooded the pool. An abundant population of *Eubranchipus* developed, unaccompanied this year, as far as 2 large collections would indicate, by *Streptocephalus*. No summer flooding occurred in 1953.

The basin filled early the following winter. A large population of larval *Eubranchipus* was observed on November 22, 1953, and during the ensuing 3 months this species alone was collected on 5 successive visits. In early March, 1954 the survivors of the *Eubranchipus* population were still present together with a very few specimens of *Streptocephalus* of such size (25-27 mm) that it seems highly probable that they had hatched at the same time as the *Eubranchipus*. On April 15, shortly before the pool dried, only a few specimens of *Streptocephalus* could be found and no *Eubranchipus* were present.

In summary, then, winter flooding of these forest pools appears to result in hatching of the eggs of both species. By the time the larvae have reached identifiable size (5-6 mm) the streptocephalids have been eliminated by some factor or factors not yet recognized, or have been so reduced in numbers that diligent sampling reveals at most only a very few individuals. Summer filling of the basins, on the other hand, probably does not result in hatching of *Eubranchipus* eggs. No individuals of this species have ever been taken during the summer months. Furthermore it would seem unlikely that the recurrence of large *Eubranchipus* populations, winter after winter, could continue if even occasional summer flooding of the basins led to hatching of larvae which must inevitably die, by reason of unfavorably high temperatures, before reaching maturity.

Hatching period; growth rate; egg production

On two occasions (January, 1952 and November, 1953) large populations of *Eubranchipus* larvae were observed to be present within 48 hours following flooding of the basins. The hatching period is thus similar to that reported for *S. sealí* under both field and laboratory conditions (Moore 1955, 1957).

Since the basins usually fill in progressive stages, the older populations are frequently of mixed sizes. One series of 7 collections, however, was obtained following nearly maximal flooding; it is believed that this population consisted for the most part of shrimp of nearly uniform age. Growth rates, based on measurements of 15-25 individuals

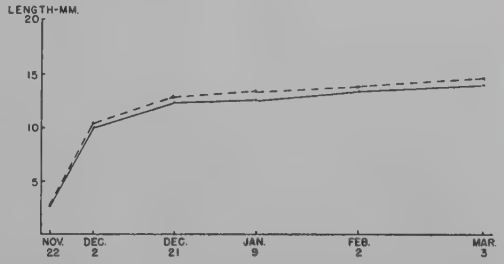

FIG. 3. Growth rate, *Eubranchipus holmani*. Solid line, males; broken line, females.

of each sex, are illustrated graphically in Figure 3.

Larval shrimp (unsexed) less than 2 days of age were collected on November 22, 1953. Total body length ranged from 2.25 to 2.75 mm. Ten

days later, during which time both sexes grew at the rate of approximately .76 mm per day, the animals were nearly mature although none of the females were carrying eggs. On December 21, at an age of about 30 days, males averaged 12.4 mm in length; females, 12.8 mm. This disparity of size in favor of the females persisted throughout the subsequent life of the population. Size increment during this interval was .13 mm per day for males and .14 mm per day for females. Ten of the 15 females examined were carrying mature, brown-shelled eggs—from 8 to 39 per female with a mean number of 27.

Growth then continued at a very low rate for the life of the population. Between December 21, 1953 and March 3, 1954 the daily increment of growth for both sexes averaged only .02 mm. Egg production likewise declined until nearly the end of the life span. On January 9, 6 of 15 females bore an average of 13 eggs (range: 12 to 18); on February 2, 5 of 15 carried an average of 11 eggs (range: 9 to 16); on March 3, 3 of 15 females bore, surprisingly enough, an average of 38 eggs (range: 32 to 43). It is perhaps noteworthy that these 3 females were among the smallest (from 13 to 14 mm) of a lot which ranged up to 16 mm in length and which averaged 14.3 mm. Quite possibly these ovigerous females were younger individuals, hatched subsequent to the main population, and were still in the early, prolific stage of egg production at the time of the collection.

A final visit was made to this habitat on April 15, 1954. Diligent collecting revealed no *Eubranchipus* and only 2 specimens *of Streptocephalus* were taken.

The growth curve for *Eubranchipus* resembles that of *S. seali* (Moore 1955) during the winter season in being characterized by an initial period of very rapid growth (.76 mm per day for the former as compared to an average of .5 mm and a maximum of 0.7 mm for the latter), followed by a period of marked retardation as egg production commenced. Unlike *Streptocephalus,* which then exhibited a second period of accelerated growth followed by a gradual decline, *Eubranchipus* continued to increase in length at a very low but more or less constant rate for the remainder of its life span.

Egg production in *Streptocephalus* was reported to commence on a limited scale during the period of growth retardation. Summer populations of this species continued to produce eggs at an increasing rate throughout the life span; during the winter season, however, egg production declined from this initial rate, then resumed at a greatly accelerated rate later in the life cycle. *Eubranchipus* females, on the other hand, displayed maximum productivity on the attainment of sexual maturity. The number of producing females and the mean number of eggs per female then showed a progressive decline until the very end of the life cycle. The apparent resumption of high productivity by a few females at the end of the cycle may be real, or it may, as previously suggested, merely indicate the attainment of maturity of members of a second brood.

Interrelationships of Eubranchipus *and* Streptocephalus *in mixed populations.*

A problem of particular interest posed by the observations herein recorded is that of the factors involved in the reduction or elimination of streptocephalids from these forest pools during the winter season. Study of this problem is planned for the future; at present no basis exists for firm conclusions. A few pertinent observations may, however, be in order.

There can be little doubt that winter flooding of the basins results in an extensive hatch of eggs of both species. For example, a very few specimens of *Streptocephalus seali* are frequently found in well developed *Eubranchipus holmani* populations. When, as is usually the case, individuals of both species are of approximately the same stage of development, the implication is that the species have coexisted since the initial filling of the pool. Further, on November 22, 1953, a number of unidentified larvae from a newly-flooded forest pool were placed in habitat water in a laboratory aquarium. On December 4, 12 days later, a collection of over 400 specimens from the same pool were all *Eubranchipus.* The 3 survivors in the laboratory culture were found to include both *E. holmani* (1 male, 1 female) and *S. seali* (1 male).

Difference in hatching time of the eggs is probably not a factor in this interspecific relationship since large hatches of the eggs of both species normally occur within 48 hours after immersion. Differential early growth rates may, on the other hand, be of some importance. Available evidence would indicate that during the first 2 weeks of life (at these winter temperatures) *Eubranchipus* grows more rapidly than *Streptocephalus.*

Although *S. seali* grows at a greater rate and attains sexual maturity much sooner at summer temperatures, it should be noted that the species is by no means seriously inhibited by low temperatures. In fact, flourishing populations of *Streptocephalus* are frequently to be found in exposed roadside ditches during the winter months, only

a hundred yards distant from a shaded forest pool which harbors an abundant *Eubranchipus* population.

Summary

1. The nomenclatorial history of the fairy shrimp, *Eubranchipus holmani* (Ryder), is reviewed and the distribution of the species is summarized. *E. holmani* has been recorded from 10 states, all east of the Mississippi River.

2. Two morphological types are represented in these collections. The form characterized by males which possess an armature of a double row of dorsal spinous processes on the thorax and abdomen appears to be confined to the extreme southernmost part of the range of the species.

3. *E. holmani* is known in Louisiana only from a few densely shaded, brown-water, cypress-sourgum ponds in eastern St. Tammany Parish. These ponds are acidic (pH 4.9 to 5.4); total alkalinity is low (5.0-8.0 ppm); the water is clear and highly colored (140-360).

4. *E. holmani* is a cool water dweller, never having been taken at temperatures above 21°C. It has been collected in Louisiana only during the winter months (November-March).

5. These forest pool habitats occasionally support mixed populations of *Eubranchipus holmani* and *Streptocephalus seali* during the winter months. During periods of summer flooding only *Streptocephalus* has been found in the pools.

6. Hatching of the eggs of *E. holmani* occurs within 48 hours after immersion. Initial growth is rapid, averaging .76 mm per day for the first 10 days. The growth rate subsequently declines to an average of only .02 mm per day, though it does not cease entirely. Females grow slightly faster and attain a larger size than males.

7. A population of *E. holmani* was observed over a period of 14 weeks, which probably represents the maximum life span. At the end of this time males averaged 13.7 mm in length, females 14.3 mm.

8. Egg production, which commences after the tenth and before the thirtieth day, is maximal at first. The proportion of ovigerous females in the population and the productivity per female appear to decline later in the life cycle.

9. The more rapid initial growth rate of *Eubranchipus* is cited as a factor which may be involved in the reduction or elimination of *Streptocephalus* from mixed populations in these forest pool habitats during the winter season.

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References

Creaser, E. P. 1930. The North American phyllopods of the genus *Streptocephalus*. Occ. Pap. Univ. Michigan. Mus. Zool., **9**: 1-10.

Daday, E. 1910. Monographie systematique des Phyllopodes Anostraces. Ann. Sci. Nat. (ser. 9). **11**: 91-492.

Daggy, T. 1952. Records of fairy shrimp in North Carolina. Journ. Elisha Mitchell Sci. Soc., 68.

Dexter, R. W. 1953. Studies on North American fairy shrimps with the description of two new species. Amer. Midl. Nat., **49**: 751-771.

———. 1956. A new fairy shrimp from western United States, with notes on other North American species. Journ. Wash. Acad. Sci., **46**: 159-165.

——— and **C. Kuehnle.** 1948. Fairy shrimp populations of northeastern Ohio in the seasons of 1945 and 1946. Ohio Journ. Sci., **48**: 15-26.

Fowler, H. W. 1912. The Crustacea of New Jersey. Ann. Rept. New Jersey State Mus. 1911, Part 2: 31-650.

Herrick, C. L. 1885. Metamorphosis and morphology of certain phyllopod Crustacea. Bull. Sci. Lab. Denison Univ. Vol. 1: 16-24.

Herrick, C. O. and **C. H. Turner.** 1895. Synopsis of the Entomostraca of Minnesota. Geol. and Nat. Hist. Surv. of Minn., Zool. Series 11, St. Paul, Minn.: 1-525.

Linder, F. 1941. Contributions to the morphology and the taxonomy of the Branchiopoda Anostraca. Zool. Bidrag fran Uppsala, **20**: 101-302.

Mattox, N. T. 1936. A new fairy shrimp belonging to the genus *Pristicephalus*. Amer. Midl. Nat., **17**: 950-953.

Moore, W. G. 1951. A fairy shrimp new to Louisiana. Amer. Midl. Nat., **46**: 255.

———. 1955. The life history of the spiny-tailed fairy shrimp in Louisiana. Ecology, **36**: 176-184.

———. 1957. Studies on the laboratory culture of Anostraca. Trans. Amer. Microsc. Soc., **76**: 159-173.

Packard, A. S. 1883. A monograph of the phyllopod Crustacea of North America, with remarks on the Order Phyllocarida. Twelfth Ann. Rep. U. S. Geol. and Geogr. Surv. of the Terr. for 1878, Part 1: 295-592.

Pearse, A. S. 1918. The Fairy Shrimps (Phyllopoda). Ward and Whipple, Fresh-Water Biology. John Wiley & Sons, N. Y.: pp. 661-675.

Pennak, R. W. 1953. Fresh-water Invertebrates of the United States. Ronald Press, N. Y.: pp. 1-769.

Ryder, J. A. 1879. Description of a new species of *Chirocephalus*. Proc. Acad. Nat. Sci. Phila.: 148-149.

Underwood, L. M. 1886. List of the described species of fresh-water Crustacea from America north of Mexico. Bull. Illinois State Lab. Nat. Hist., Vol. 11, Art. V: 323-386.

SPECIES ABUNDANCE AND COMMUNITY ORGANIZATION

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The prevalent conviction among ecologists that natural communities represent important and meaningful assemblages of organisms has prompted a diverse series of analyses. The present paper is an examination of some of the analyses as applied primarily to soil arthropods, with an explanation of some of the difficulties that have been encountered. The thesis contained herein is that the numerical abundance and spatial distribution of all species found must be taken into account before an understanding of community organization can be obtained.

Analyses and definitions of the community have been used to approach the subject from several more or less distinct points of view—function, location, and biotic composition. Most studies have dealt with only one of these aspects, but some assumption has usually been made about the others. Macfadyen (1957) has recently reviewed the various community definitions that have been offered. In the present paper, particular attention is paid to the aspects of community structure that can be discovered from the occurrence and relative abundance of species, usually confined to a taxonomic group not larger than a phylum.

The species composition of communities has been used as an approach to community analysis for at least 50 years. The data have been viewed from the standpoints of species frequency, species per unit of area, the spatial distribution of individuals, and the numerical abundance of species. In all of these, attempts have been made, graphically and mathematically to express some aspect of community structure.

Species Frequency

The regular arrangement of species in a community was apparently first observed by plant ecologists (Raunkiaer 1909, 1918, 1934; Gleason 1920). In Raunkiaer's analysis, the frequency of occurrence of each species in a series of samples provides the basic data. When the number of species in each frequency class is plotted, there usually results a curve more or less resembling a reversed "J" (Kenoyer 1927). The original interpretation was that the short arm of the curve, representing species present in 80% or more of the samples, were the dominant forms which were able to prevent immediate competitors from occupying the area, while the long arm of the curve consisted of non-dominants that did not offer competition. It was eventually shown, however, that the shape of the curve depended upon sample size, and that species tended to shift position between the two arms as the samples were made larger or smaller (Romell 1930).

Association of Common Species

As an outgrowth of the species frequency studies, there has developed a school of "biocoenology," which uses differential association of a number of relatively ubiquitous species in order to delimit communities. The details of the method vary with different workers, some using numerical abundance in addition to common presence. Because of the dependence of ubiquity on sample size, the selection of the species used must be somewhat arbitrary, and to this extent the method is artificial, although interesting results may be obtained (Macfadyen 1954, 1957; Kontkanen 1957, Whittaker and Fairbanks 1958). Conventionally, the results are expressed in a "trellis diagram," which is obtained by rearranging the list of samples until the maximal affinities between samples are obtained.

An alternate method of using the association of relatively ubiquitous species to delimit communities has been described by Hairston and Byers (1954).

Species per Unit of Area

In order to avoid the arbitrary restriction imposed by selecting common species, a number of plant ecologists have concentrated upon the relationship between the number of species found and the area covered. This has resulted in the "species area curve" (Arrhenius 1921, Gleason 1922, Cain 1938). Using the curve, an approach can be made to the most favorable size of sample for the conditions of any given study. The number of species found apparently increases linearly with the logarithm of the area studied over a wide range of sample sizes, and the slope of the line thus formed has been used as a measure of community diversity (Margalef 1957), although the relationship does not hold for very small samples (Hairston and Byers 1954), and is claimed not to hold for very large ones (Preston 1948). Shinozaki (1955) and Shinozaki and Urata (1953) have expressed doubts as to the ecological significance of the relationship.

Spatial Distribution

Although some earlier workers were aware that the obvious non-random distribution of organisms in nature must have an effect upon the results of sampling, Cole (1946 a and b) was apparently the first ecologist to attempt a measurement of the nature of the distribution of animals, and of the interspecific associations that could be discovered by appropriate statistical tests. A series of authors (Neyman 1939, Anscombe 1948, 1949; Thomas 1949, Thomson 1952, Bliss and Fisher 1953) have reported mathematical descriptions of observed distributions. The underlying causes of the observed non-random distributions are different from species to species, and therefore none of the mathematical formulae are valid for all cases. The negative binomial has certain practical advantages for the ecologist, who may have neither the time nor the inclination to do more than use the formulae as presented. Its usefulness lies in the fact that there are published formulae for estimating the necessary terms (Bliss and Fisher 1953, Bliss and Calhoun 1954). This distribution contains a constant (k), the value of which can range from zero at maximal clumping to infinity at completely random distribution. It is thus of considerable value in estimating the relative degree of clumping shown by different species.

Another method of expressing the spatial distribution of organisms is as the mean distance to the nearest individual of the same species (usually referred to as the "nearest neighbor" method) (Dice 1952, Clark and Evans 1954, Thompson 1956, Blackith 1958). The technique is especially applicable to distributions of plants and of those animals having nests or burrows.

The influence of the spatial distribution of constituent species on analyses of community structure was pointed out by Hairston and Byers (1954), who interpreted the failure of indices of diversity to remain constant with increasing sample size as being due to the clumping of rare species. More information will be given on this point below.

Numerical Abundance

The first important attempt to interpret animal community structure from the relationship between the numbers of individuals and of species obtained by sampling was that of Fisher, Corbet, and Williams (1943). These authors started from the observations that a regular curve results whenever sampling data are plotted so as to compare the number of species in the successive abundance categories. There are many species with a single individual, fewer with two individuals, and so on to higher numbers, only a few species being represented by very large populations. Thus, in their large collection of moths from light traps, consisting of 15,609 individuals distributed among 240 species, the 12 species represented by 282 or more individuals constituted over half of the collection, while over half of the species were represented by 13 or fewer individuals. The arithmetic plot of the data resembles a hyperbola, but on a geometric plot, the hyperbola can be shown not to apply.

Fisher concluded that the logarithmic series provided an adequate description of the data. The logarithmic series is a special case of the negative binomial distribution in which k is assumed to be equal to zero. As he points out, it is possible to make this assumption if the number of undiscovered species is unknown and the series cannot go below one individual per species. This requires the addition of a new constant *alpha,* and the relationship between the number of species S and the total number of individuals N can be expressed by the formula

$$S = \alpha \ln \left(1 + \frac{N}{\alpha}\right) \qquad (1)$$

The constant, α, thus becomes an expression of the diversity of species in relation to the total number of individuals. Fisher, Corbet, and Williams found that for the light trap data the value of α was more or less constant over a range of sample sizes, and concluded that it was a valuable index of the diversity of species in a natural community.

The logarithmic series was later applied to a variety of situations by Williams. Some of these situations were the number of species per genus in a taxonomic group (Williams 1944, 1947a), the number of publications per scientific author (Williams 1947b) and many other similar series. The curve seems to apply to almost any situation involving duplication, selection, and dispersal.

Preston (1948) proposed a different method of representing the same data. Objecting to that feature of the logarithmic series requiring more species of minimal abundance (one individual) than any other category, he pointed out that for such well known groups as birds, there appear to be no more very rare species than very abundant ones, and that most species seem to have an intermediate position. He found that when the species in a census are grouped into abundance categories (octaves) representing all of the numbers between successive powers of 2, the number of species in the octave form part of a normal curve, which can be expressed as

$$S_r = S_o e - (ar)^2 \qquad (2)$$

where S_o is the number of species in the modal octave, S_r is the number of species r octaves from the mode, and a is a constant calculated from the data. Complete data being unobtainable in most cases, the curve obtained is truncated at the rare end, but the complete form is predictable, and hence the total number of species, including those as yet undiscovered. In a later paper, Williams (1953) accepted the greater utility of Preston's lognormal analysis, although the logarithmic series is preferable mathematically. Brian (1953) has observed that the curve obtained from Preston's method is, in many cases, more similar to the negative binomial than to the normal. In the present author's opinion, however, the fit is seldom sufficiently good to make the distinction.

A number of other indices of diversity have also been proposed (Numata 1950, Margalef 1951, 1956).

Hairston and Byers (1954) attempted the analysis of extensive data on soil arthropods by both the logarithmic series and the lognormal method. They concluded that both indices of diversity were related to sample size, a feature that renders impossible the comparison of different communities. The suggested reason was the clumping of rare species so that, with repeated or enlarged samples, there is more likelihood of encountering new rare species than additional specimens of species already found. The phenomenon was more apparent in their data than in the earlier publications because the samples came from fixed points in the community, whereas the clumping of individual species is largely obscured in their passage to a light trap.

Information Theory and Community Analysis

In a long and thoughtful article that will repay careful reading, Margalef (1957) has considered the possibilities of analyzing natural communities by the approach of information theory. Information in this sense is a function of the number of possible choices between equally probable states required for a complete understanding of the level of organization under consideration. The assumption of equally probable states is, of course, entirely too restrictive for serious use in most ecological studies, but the theory contains certain concepts that will be used below, and that make it worthwhile presenting in some detail. Thus, we may consider the information in a community, as based upon counting the number of species present, or we may consider at a different level the amount of information as based upon placing all individuals in their proper species, or, finally, we may consider the total possible information in the system, considering each individual as separately identifiable and localizable in space. In each case, what is measured is a function of the number of choices required to reduce the total number to a given lower level, and in the final case to reduce it to a single choice. Since the possible number of combinations among N individuals is N!, the total measured information would be a function of this, or expressed in "bits" (the usual unit in information theory),

$$I = 1.443 \ln N! \qquad (3)$$

In most cases, the data are such that this is not very meaningful, since we know too little about the spatial arrangement of individuals, to say nothing of their individual identification. The placing of individuals in species is usually the most that can be hoped for, and the information in the system is:

$$I = 1.443 \ln \frac{N!}{N_1! N_2! \ldots N_S!} \qquad (4)$$

in which N_1, N_2, etc. are the numbers of individuals in the different species. Information theory thus makes no pretense of providing an explanation for observed phenomena, but only tells how much information is required to explain them. It will be recognized immediately that this is a very large amount, and in practice becomes impossible to calculate for samples of any respectable size. Various approximations have been proposed to circumvent the factorials.

One of the most important points in Margalef's paper concerns the concept of redundancy. This derives from the obvious fact that the information at the level of placing individuals in their proper species depends upon the relative abundance of the species. In the improbable event that all are equally abundant, the denominator is small and the measured information is maximal; if individuals are distributed completely at random among the species, the information is less but still considerable, and if, as is usually the case, the abundances are very unequal, the denominator of the fraction is large, and the information in the system is much less.

The inequality of abundance constitutes repetition for the common species, and since this increases the probability that an individual belongs to a species already recognized, the amount of information per individual is relatively small. This repetition is what is meant by redundancy. We come at this point to a stumbling block caused by the restricted use of the familiar word "information." It is difficult, as Margalef says, to visualize how a random arrangement could contain

more information than a non-random one, but if it is remembered that information is measured as a function of the number of choices required to reduce the system to a given level of organization, then it is clear that more choices are needed to describe a random arrangement than an organized one. The difference between the two can be considered as a measure of the degree of organization that has gone into setting up the observed system, although it is a weakness of the information theory approach that it is not possible to say anything about the system prior to its organization, and assumptions either of randomness or of some other arrangement are necessary.

Margalef rightly considers that the direct formulae are unworkable, and uses instead a simple index of diversity derived from the above-mentioned linear relationship between number of species and the logarithm of the size of sample (or of total individuals). Thus,

$$d = \frac{S - 1}{\ln N} \qquad (5)$$

He makes a comparison between the results obtained with this formula and 2 others derived from information theory, and concludes that the simple index will give satisfactory results. The comparison is based not on an actual series of species counts, but on the frequencies of letters in a sentence in Spanish, part of a sentence in English, and a series of random numerals. His justification of the simple index is based upon the fact that all 3 indices become stable after a sharp rise in response to a new system of symbols. The comparison between the letters in a language and the arrangement of organisms in a community is not valid, however, as will be shown below.

Models Derived from Biological Premises

Dissatisfied with empirical mathematical descriptions, MacArthur (1957) proposed that the situation be viewed from the standpoint of what is or could be happening biologically in the community. Using the relative sizes and possible arrangements of niches held by the species in a community, he pointed out that conceivably these could be completely separate, adjacent, or overlapping. On the assumption that the total number of individuals is equivalent to the occupancy of the whole environment, and that the species represent the niches, MacArthur presented mathematical models representing the functional community as broken at randomly distributed points into contiguous, non-overlapping niches for one hypothesis, or by randomly distributed pairs of points into overlapping niches for a second hypothesis, or into separate units of randomly distributed sizes (discrete niches) for a third hypothesis. He gave data from a bird census (and mentioned others) that the first hypothesis fits. The second and third hypotheses do not appear to have validity in any situation yet tested.

For the first hypothesis, the predicted abundance of the rth rarest species may be calculated as:

$$\frac{N}{S} \sum_{i=}^{r} \frac{1}{(S-i+\ )} \qquad (6)$$

where N is total individuals, S is total species, i is the interval between successively ranked species and the rarest, and r is rank in rareness.

With regard to the first hypothesis, MacArthur found that bird censuses from large areas departed from the model in that common species were more common than predicted, and rare species rarer. When small parts of the large area (individual habitats) were censused, the fit was considerably better. He postulated that a non-fit of the sort that he found represents heterogeneity, while in homogeneous habitats the relationships conform to his hypothesis. A few other kinds of data have been applied to the hypothesis (Hutchinson 1957), and some seem to fit, particularly marine gastropods of the genus *Conus* (Kohn, quoted by Hutchinson).

Observations

Most of the data used in this study concern soil arthropods, obtained by Tullgren extraction. The site of the collections is an abandoned field on the Edwin S. George Reserve of the University of Michigan. It had remained undisturbed by man for at least 25 years and unploughed for 50 years prior to the sampling. Deer pressure has apparently prevented succession to woody vegetation. The otherwise quite uniform area is interrupted by 12 small depressions, referred to hereafter as "swales," characterized by a dense mat of blue grass (*Poa pratensis*), in contrast with the upland which is dominated by *Poa compressa* and *Aristida purpurascens*. For a more detailed description of the vegetation, see Evans and Cain (1952), and Cain and Evans (1952). The microarthropods were extracted from 2 series of samples, one taken at random over the upland part of the field, and the other taken at random from the swales. All samples consisted of cylindrical cores, 5 inches in diameter and 8½ inches deep. The complete data from 38 of the upland samples are given in Hairston and Byers (1954). Five samples from one of the 2 largest swales have now been sorted and counted, and the results are

TABLE I. Number of specimens of all microarthropods obtained by Tullgren extraction of samples from upper 8½ inches of soil in a single swale. Collections made 1949-1950

Species		Date of Sampling				
		Sep. 9	Oct. 20	Nov. 17	Dec. 8	Jan. 12
Araneida	U4	2	0	0	0	0
	U7	0	1	0	0	1
Pseudoscorpionida	U1	1	2	4	1	0
Acarina	P1	6	0	71	206	128
	P3	0	0	0	0	1
	P4	0	2	0	0	0
	P5	4	1	7	4	10
	P8	0	2	0	0	0
	P10	9	0	0	0	0
	P11	13	51	0	2	1
	P13	1	1	1	0	3
	P14	24	0	1	3	1
	P15	1	0	0	0	0
	P16	1	0	4	1	0
	P17	44	0	0	0	0
	P18	0	0	15	48	0
	O1	260	67	15	608	240
	O2	505	21	140	87	40
	O4	0	0	0	31	12
	O5	52	3	135	39	2
	O6	0	0	0	404	134
	O7	6	1	0	0	0
	O9	355	122	119	534	340
	O11	0	0	0	8	22
	O12	37	0	1	6	0
	O14	3	0	0	0	0
	O18	0	0	0	55	21
	O20	0	1	0	0	0
	O23	28	98	17	32	49
	O31	61	21	0	19	44
	O32	21	26	3	2	3
	O33	30	162	121	108	59
	O34	2	1	0	2	0
	O35	475	774	2286	493	775
	O36	0	0	5	4	0
	O37	1	0	2	8	0
	O38	1	0	0	0	0
	O39	0	0	174	12	0
	O40	0	0	11	2	30
	O41	0	0	1	0	0
	O42	0	0	3	0	27
	O43	4	0	1	24	1
	O44	0	0	0	1	0
	O45	0	0	0	6	12
	O46	0	0	0	0	2
	O47	0	0	0	0	2
	S2	0	0	0	0	36
	S5	8	2	33	55	25
	S6	0	0	59	0	4
	T1	0	0	0	2	5
	T7	1	1	0	5	11
	T10	0	2	0	10	1
	T12	54	49	0	18	6
	T13	0	1	1	0	1
	T14	0	0	0	7	3
	E1	73	31	104	112	99
	E2	49	9	106	26	66
	E3	0	3	0	0	0
	E4	0	0	0	5	0
	E5	0	11	0	0	0
	E6	4	9	6	44	120
	E8	15	9	1	0	3
	E11	0	1	0	0	1
	E13	9	0	0	11	3
	E18	0	0	0	6	10
	E24	0	0	0	5	2
	E27	13	18	11	9	27
	E34	1	0	12	0	0
	E38	0	8	26	10	3
	E42	0	0	4	0	0
	E43	0	0	2	0	0
Diplopoda	U1	1	0	1	0	0
Pauropoda	1	4	35	4	3	0
Symphila	1	0	0	1	1	5
Hexapoda Protura	1	0	15	9	9	1
	2	0	0	2	0	0
	3	0	0	5	0	1
	4	1	0	0	0	0
Thysanura	J1	0	2	0	1	0
Collembola	P1	0	8	0	5	1
	P2	13	6	10	5	154
	P4	0	0	0	3	4
	P5	0	0	0	18	15
	P14	0	1	1	24	6
	P15	0	1	0	0	0
	P16	20	0	6	21	16
	P17	0	0	8	420	42
	E1	1	0	0	3	5
	E2	0	0	0	6	11
	E4	57	26	16	0	58
	E5	0	0	9	4	23
	E6	0	0	0	1	3
	S3	0	1	0	0	6
	S4	0	0	0	1	0
	S5	9	0	4	0	0
Corrodentia	A1	2	0	0	0	0
Thysanoptera	6	33	0	0	8	6
	11	5	1	0	2	2
	16	2	0	0	0	0
Hemiptera	L1	0	0	1	0	0
	D1	0	0	0	0	1
Homoptera	Ny1	0	2	1	1	0
	Ny3	0	1	0	0	0
	Ny9	0	0	3	0	0
Coleoptera	St6	1	0	1	0	0
	St7	0	0	1	0	0
" Larva	4	0	0	0	0	1
	15	0	7	12	2	1
	16	2	0	2	2	0
Lepidoptera	L10	13	10	22	3	1
Diptera	L11	2	0	0	0	2
	L12	1	0	1	0	0
Hymenoptera	F1	0	1	0	0	0
	F3	0	1	0	0	0
	F4	0	1	0	0	0
# OF SPECIES		54	51	57	66	69
# OF INDIVIDUALS		2341	1631	3622	3618	2757

given in Table I. The unconventional classification has been described and defended in the paper referred to. As will be shown below, this classification yields data that have the same characteristics as more conventional and time-consuming methods. The same designations are used in Table I that were used in the earlier publication, the numerical series being continuous with the designations already used.

The data, as might be expected, resemble those from the upland samples taken at the same time. There are more species and more individuals than are found in the samples from the upland, but there is overlap in the values for individuals.

Clumping and Abundance

In analyzing the upland samples by the logarithmic series and the lognormal distribution, Hairston and Byers found that the results depended upon the size of the sample under consideration, and, as noted above, postulated that clumping of the rare species could account for this, since new rare species would then be more likely to be added than individuals of other rare species already encountered. They were able to show that some of the rare species were clumped, but were unable to obtain estimates of the degree of clumping. Reasonable methods for estimating the constants of the negative binomial distribution are now available (Bliss and Fisher 1953), and the constant k has been estimated for all species represented by two or more individuals (Figure 1). It should be pointed out that the estimates are less than 90% efficient in many cases, but the trend of the values in relation to mean abundance is so apparent that the low efficiency cannot be considered a series objection to the conclusions.

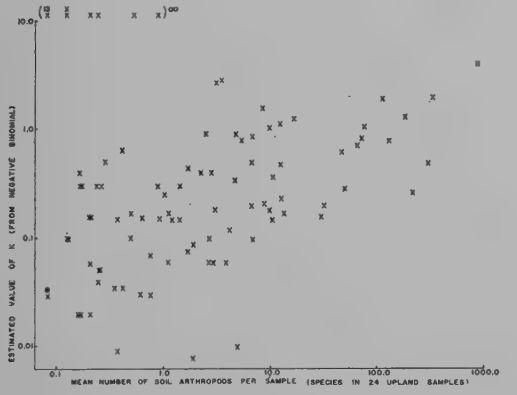

FIG. 1. The inverse relation between abundance and clumping as measured by the constant k in the negative binomial distribution. Data from Hairston and Byers (1954).

Since a small value of k denotes clumping, and a value of infinity denotes randomness, 83% of the species show some degree of clumping, and there is a definite, even trend toward more intense clumping as rarer and rarer species are considered. It will also be observed that all of the randomly distributed species are relatively rare, all having means of less than one individual per sample. Two thirds are represented by only 2 individuals each. This suggests that with further sampling many of them would also be found to be clumped.

The data from the 5 swale samples have been treated in the same fashion (Figure 2). As might be expected from the smaller number of samples, the points on the chart are more scattered, but the same trend is evident, being significant at the 1% level when tested by tetrachoric r (Dixon and Massey 1951, p. 233).

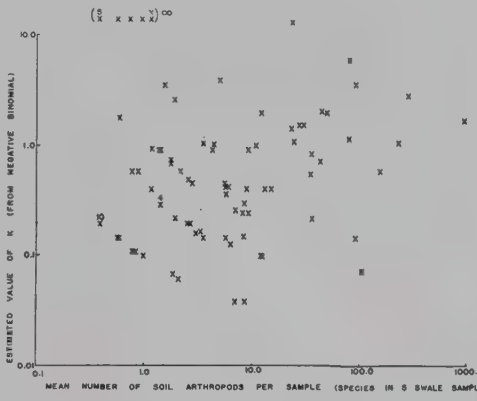

FIG. 2. The inverse relation between abundance and clumping as measured by the constant k in the negative binomial distribution. Data on swale samples from Table I.

The progressive clumping of rarer species gives an indication of the structure and organization of the communities studied. It appears that the suitability of the different parts of the community is far from uniform when the different levels of abundance are considered. The more nearly the whole community is suitable for a species, the more abundant that species is, and the more likely it is to have a random distribution. Conversely, the rarer a species is, the more likely it is to be strongly clumped because it only finds suitable habitat in a few places in the community. Between the extremes, a complete series of intermediates is found. It is this continuous series that has caused considerable disagreement among ecologists concerning the structure and even the objective existence of communities. Some have been impressed with the homogeneity of the community, and they were influenced by the common presence of the abundant species over the whole community; others have been impressed by the mosaic nature of the community, and were influenced by the strongly clumped distributions of the less abundant species. The picture is more likely one of a continuous series of mosaics, each overlapping the others and with larger and larger pieces, until for the most abundant species the whole community is one piece—a part of a mosaic biosphere.

Comparison of the Two Communities

If the above interpretation is correct, an examination of the fates of the species common to the 2 communities should yield interesting information. For the months for which swale data are available (September to January), 90 species were recorded from the 5 upland samples nearest the swale, and 116 species were recorded from the 5 swale samples. There were 43 species common to the two communities, which amounts to 48% of the upland species and 37% of the swale species. This result might have been anticipated, as the swales are moist, rich islands in the sandy upland. It is of greater interest to note that the relation between numerical abundance of the different species in the 2 communities (Figure 3) is weak, al-

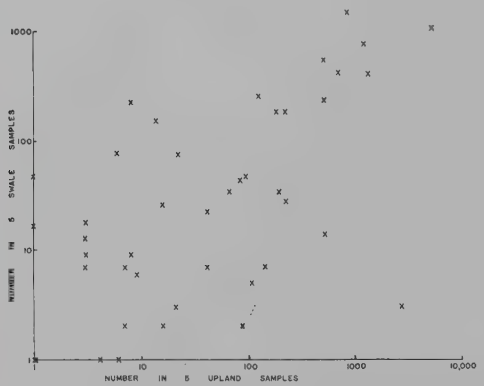

FIG. 3. The relative abundance of species in two similar adjacent communities. Each point represents one species found in both swale and upland.

though it is significant statistically. This is to be expected if the general conditions in the 2 places are somewhat different. Species adapted to conditions in the swale would be able to find suitable habitats only in restricted parts of the upland, and vice-versa. This is borne out by comparing the abundances and the values of k for each species in the 2 communities. The comparison is meaningless for species which have only 1-3 individuals in one or both communities, but 21 of the 27 species with better representation in both communities show greater clumping in the community of less abundance (Table II). The table also shows that the tendency is strongest where differences in abundance are greatest, and hence least likely to be artifacts of sampling error. This indicates that the degree of clumping is not necessarily a character of the species, but also depends upon the kind of community in which it is being studied. The foregoing conclusion would probably not hold, of course, for social or territorial species.

TABLE II. The relation between relative abundance and relative degree of clumping in 27 species of soil arthropods found in 2 communities. For the value of N_1/N_2, the smaller number was chosen for the numerator, regardless of community. This operation fixed the positions of k_1 and k_2. A lower value of k denotes greater clumping.

Relative abundance (N_1/N_2)	Number of cases	Number of Cases in Which k_1/k_2 Was:	
		Greater than 1	Less than 1
0 -0.33.....	11	0	11
0.34-0.66.....	10	3	7
0.67-1.00.....	6	3	3
Totals.....	27	6	21

Diversity, Heterogeneity, and Community Identification

Using equation (5) above, Margalef has made some interesting interpretations of his data on marine phytoplankton. He recognized that, like other indices of diversity, this one shows an increase with enlarged samples. He did not regard this as a serious objection, and pointed out the circular argument accompanying descriptions of most such indices. These are judged valid when they can be shown to remain stable in "reasonably homogeneous" communities, but there is no criterion of homogeneity other than the index that is described. He attributes the increase in the value of the index with increased sample size to a real heterogeneity.

Margalef's justification for the use of his index is based upon the frequently-noted similarity between the distributions of letter frequencies in a language and species frequencies in samples from communities. Selecting most of a sentence from his own text, he calculated the index of diversity for successively larger samples, starting with a single letter. The index rose rapidly at first, but after 30 or 40 letters it became quite stable. In addition to his own index, he used 2 others derived directly from information theory, and he considered that the fact that all 3 indices followed the same pattern in analyzing the languages constituted justification for their use in analyzing data from natural communities. The analogy with language is interesting, but unless common or similar underlying causes can be shown for the organization of languages and communities, any similarities must remain interesting coincidences, and must not be used in interpretation or in the foregoing kind of justification.

In the present case, the most likely reason for an apparent increase in heterogeneity with an increase in sample size lies in the spatial distribu-

tion of the species concerned, and the inverse relation between clumping and abundance. Accordingly, if the arrangement of letters in a language is to be used for justifying a system of analyzing a community, the distribution of the letters should show the same characteristics as the distribution of species. This is obviously not the case, but if mathematical evidence is required, it is given in Figure 4. In this case, 10 lines taken at random from Margalef's paper were used as "samples."

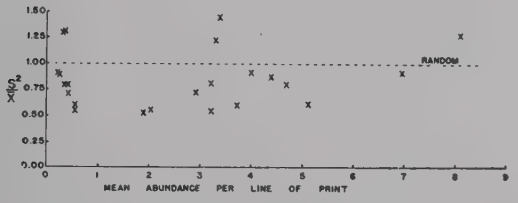

FIG. 4. The relation between clumping and abundance of 23 letters in 10 lines of Spanish text, taken at random from Margalef (1957).

Only 5 of the 23 letters showed any evidence of clumping, the remainder being slightly more uniform than random in distribution. This means that the constant k in the negative binomial cannot be used, since its value becomes meaningless for most letters. Instead, the ratio of variance to mean abundance has been used. They are equal and the ratio equal to unity when the distribution is random. Higher values denote clumping, lower ones more uniform distribution. It is clear that no relation exists between the abundance of a letter and its spatial distribution. Hence, we should expect that an index of diversity would not be related to sample size as it is for most field data, since repeats of letters already encountered would be relatively as frequent as new letters. This accounts for the stabilization of the 3 indices of diversity in Margalef's analysis. The large proportion of letters that are uniformly distributed suggests a similarity with the distribution of birds, which tends to be uniform because of their territories. Bird censuses have been particularly attractive in the justification of indices of diversity (Preston) and models (MacArthur), and it seems likely that there is a relationship between their use in such cases and their unusual spatial distribution.

Although the justification for their use is not valid, these indices gave interesting results when used to analyze plankton communities. Margalef was able to show regular gradients in diversity in an estuarine river, and found that the distribution of the gradients corresponded to the influence of incursions of water from the open Atlantic. Since the data presented in Table I above and by Hairston and Byers represent two quite different communities with two subdivisions of the upland community, attempts were made to discover whether Margalef's indices of diversity and heterogeneity could be used to separate the 3 in a completely objective manner. The method used was to calculate the diversity of pooled pairs of samples, on the theory that pairs from different communities should show greater diversity than pairs from the same community. For this purpose, 14 samples were selected: 5 from the swale, 7 from the central part of the upland, and 2 from the peripheral part of the upland. Eight of the 9 upland samples could be classified as coming from homogeneous material, since all combinations among them gave low indices of diversity.

Another series of calculations was also made, using the index of heterogeneity

$$H = \frac{d_{AB}}{d_A + d_B} \qquad (7)$$

in which d_{AB} is the index of diversity of the pooled samples A and B. These indices were high for all combinations between swale and upland samples, and lower for all combinations within either community. Neither index gave any indication of a difference among the upland samples.

It thus appears valid to conclude that the approach is adequate to effect a crude separation of samples from 2 distinct but fairly similar communities. This accounts for its effectiveness in Margalef's study of phytoplankton. In his case, of course, there would be no method of estimating beforehand which samples came from which community. In the case of the terrestrial communities, a glance at the vegetation effects an immediate preliminary classification that is as accurate as the rather laborious calculations reported.

The Biological Model

The development of a model based upon biological premises is an encouraging advance over empirical descriptions. A comparison of expected values with the observed data on soil arthropods (Figure 5) is disappointing at first glance. The fit is poor both for single samples and for pooled samples. In all cases, the observed curves are too steep—rare species are too rare and abundant species are too abundant to conform to expectations. Lest the reader conclude that the failure is due to the unconventional taxonomy, a similar set of calculations has been made for the data reported by Kontkanen (1957) on beetles, in which there appears to be no question of the taxonomic certification (Figure 6). The same kinds of deviations from the expected are found in these data, particularly for the abundant species. The appar-

ently closer fit at the rare end of the curve is due to the fact that a number of the less abundant species were omitted from Kontkanen's table. One of 5 samples from his Community I does show an excellent fit, but this can scarcely be regarded as anything more than a statistical accident, as it is clearly the exception rather than the rule.

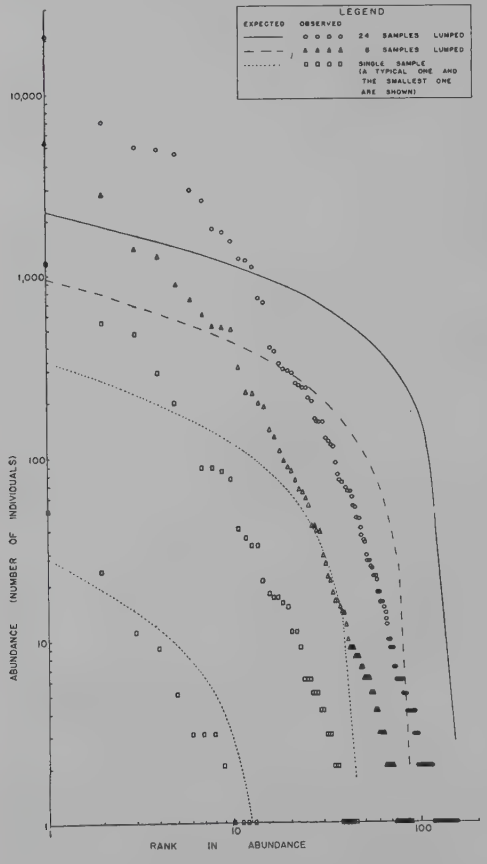

FIG. 5. The relation between abundance and rank in abundance of soil arthropods for samples of various sizes, compared with expectations based on MacArthur's first hypothesis. Data from Hairston and Byers (1954).

An examination of Figure 5 shows that there is apparently a relationship between the size of the sample and the departure from expectations. This observation is in agreement with MacArthur's statement that bird censuses from large areas show a greater departure from expectation than do those from small areas. MacArthur attributes this effect to the greater heterogeneity of the large area, and concludes that heterogeneity is indicated whenever data show this kind of departure from expectations.

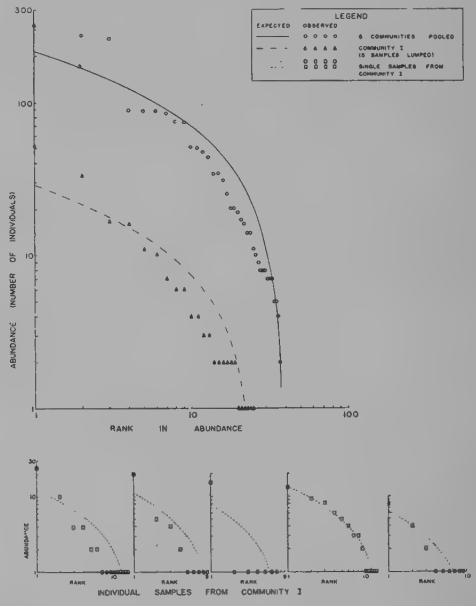

FIG. 6. The relation between abundance and rank in abundance of beetles, compared with expectations based on MacArthur's first hypothesis. Data from Kontkanen, 1957.

There are, however, certain difficulties with this interpretation, especially as regards the present data. First, although the idea that the large area represents greater heterogeneity than smaller ones is logical in the case of birds, it is less acceptable for the soil arthropods, both because the samples were selected for homogeneity on an independent basis, and because the conclusion of marked heterogeneity within a community violates well-founded ideas to the contrary. Second, there is a more general objection to the assumption of randomness in MacArthur's model. If the natural community is a meaningful assemblage of organisms, the arrangement and relative abundance of these would not be expected to be random. At this point, it is well to recall the concept of redundancy in information theory. Redundancy was shown to be indicative of organization, and also to represent departure from randomness. Thus, if the community is an organized system, one would not expect the relative abundance of the species in it to conform to a random series.

Fortunately, there is a test that can resolve the question. This is based upon the implied predictions in the two interpretations. MacArthur's

explanation predicts that if we deliberately add heterogeneous data (as from another community) to the system, the departure from expectation will be greatly increased. The prediction implied in the *a priori* assumption of organization is exactly the opposite; if data from another community are added, the organization is less, and a nearer approach to expectations based on randomness is achieved than when an equivalent amount of data from the same community is added. If we return to Figure 6, it can be seen that lumping the 5 communities present in Kontkanen's data yields a curve that seems to come closer to the expected than does data from a single community. In the absence of an objective means of comparison, however, the difference is not very convincing.

I am indebted to Mr. Peter H. Ovenburg for the suggestion that an accurate objective estimate of the deviation of a set of data from expectation can be obtained by comparing the observed with the expected variance. He has also provided the formula for calculating the expected variance in MacArthur's model:

$$s^2 = \left[\frac{N^2}{S^3}\sum\left(\sum_{i=1}^{r}\frac{1}{(S-i+1)}\right)^2\right] - \frac{N^2}{S^2} \qquad (8)$$

the terms being the same as in equation (6) above. This expression is a measure of the expected deviation from a hypothetical uniform distribution, and hence the comparison with the observed variance is a valid one. Unfortunately, the expected variance cannot be assigned a probability, and the worth of the comparison is thus somewhat subjective (Craig, personal communication). It does yield results that are internally consistent.

The ratio $\frac{\text{observed variance}}{\text{expected variance}}$ was calculated for a series of single and pooled samples as follows: the 5 upland samples nearest the swale in space and covering the same months as the swale samples were selected as being most appropriate for the desired comparison. The ratio of variances was calculated for each of these samples, and also for the larger sample formed by pooling them. The ratio for the larger sample is considerably greater than the average of the 5 individual ratios. When 5 additional upland samples are added, the ratio of variances is found to increase in an apparently linear fashion with the number of samples pooled (Figure 7). A similar relationship holds for the 5 swale samples.

The critical test of the 2 hypotheses can be made by comparing the ratios between variances obtained by pooling 5 upland and 5 swale samples and the ratio obtained by pooling the 10 upland samples. MacArthur's explanation predicts that the ratio obtained by pooling samples from the 2 communities will be the higher, whereas the explanation propounded above predicts that the ratio obtained by pooling the 10 upland samples will be greater because a greater degree of organization has been revealed. The results are given in Figure 7. Introducing heterogeneity clearly

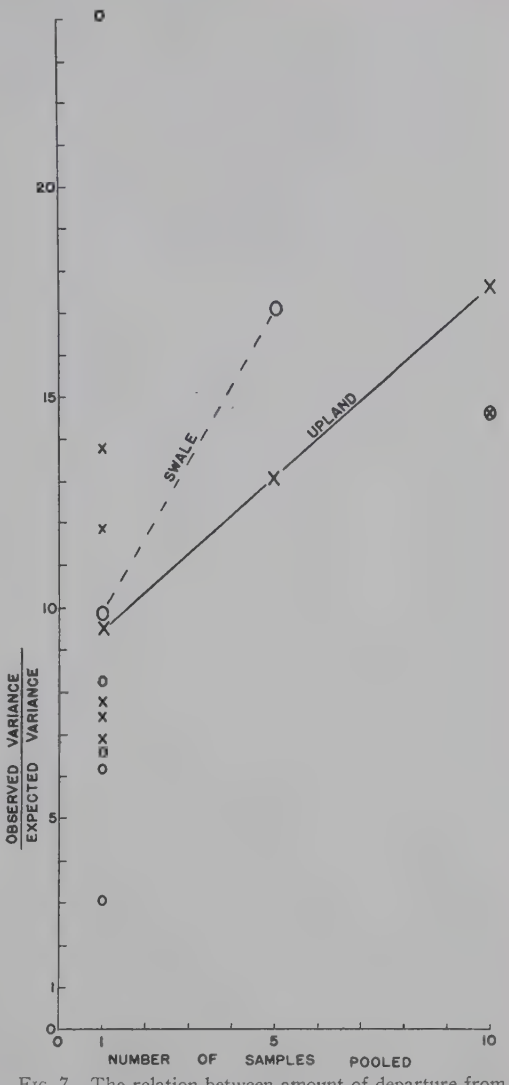

FIG. 7. The relation between amount of departure from MacArthur's model (ratio of variances) and sample size in 2 communities of microarthropods, and in a sample formed by pooling the 2 communities. Small symbols represent variance ratios for individual samples in upland (crosses) and swale (circles). Large crossed circle represents ratio of variances for a sample formed by pooling 5 swale and 5 upland samples.

reduces the ratio between variances and thus approaches more nearly the expectation of a random distribution of species populations. Adding more samples from the same community causes the deviation from randomness to increase linearly with the number of samples pooled.

The effect is even more dramatic when two completely unrelated samples are pooled. For this purpose, Margalef's Sample A of marine phytoplankton and Hairston and Byers' Sample P7-5857 of soil arthropods were used. The former consists of 1032 specimens in 21 species, and the latter consists of 494 specimens in 25 species. The observed variance is 62.36 times as great as expected for the plankton sample, and 11.76 times as great as expected for the soil arthropods. For the two samples pooled, the ratio is 7.87. Thus the more complete the heterogeneity that is added the nearer the approach to expectation based on the assumption of randomness.

Discussion

Perhaps the most satisfying means of expressing community organization would be through directly observed actions of all species present upon each other. This kind of information is not available for any community, and while such data as we have are valuable, they are much too fragmentary to allow the construction of more than the most general kind of model based on food relationships (Lindeman 1942, Macfadyen 1957). Other relationships, such as competition, are even more imperfectly known, especially in the field.

It therefore seems worthwhile to approach the subject from the viewpoint of the distribution and relative abundance of the different species, with the assumption that the 2 approaches must be interrelated in ways not immediately apparent, but ultimately discoverable. The merit of MacArthur's analysis lies in the implied relationship of species abundance to community energetics. His demonstration that the model based on the assumption of contiguous but non-overlapping niches fits the data better than models based on alternative assumptions is of considerable interest, since it implies that the factor determining population size is something that cannot be shared, but is completely utilized. Space, in the sense of "habitat niche" does not qualify, since species do share the same space and do not occupy all of it, although in a few cases 2 species have been shown to occupy virtually non-overlapping stations along an environmental gradient (Beauchamp and Ullyott 1932, Hairston 1951). Food would appear to be the only factor likely to qualify. At first thought, the apparent excess of many kinds of food (Andrewartha 1957) would appear to contradict the foregoing statement, but if we recognize that food not consumed by herbivores or carnivores is ultimately used by reducers, it is clear that the objection is not valid for the community as a whole, and that in any balanced state, such as we assume communities to be, the food is completely consumed by some species or other. In fact, this is axiomatic in biogeochemistry. Moreover, although the same species may be shared as food, a single item can only be consumed by one individual at a time. The most perplexing aspect of the analysis based on MacArthur's hypothesis is that it should be applicable to restricted taxonomic groups, so that it is apparently not necessary to consider all species in the community at once. This implies that each taxonomic group consumes all of the food that is available to it. Carrying this line of reasoning to the species level, the hypothesis of contiguous but non-overlapping niches makes good biological sense, in that no species can eat more food than is available.

If these conclusions are valid, there are implications concerning the importance of competition between species in the community. It would appear to be true that the process of adaptation of each species towards the maximal utilization of resources has resulted in innumerable competitive situations which have been resolved in various ways. If the outcome has been the elimination of some species from the system, there would be no way to demonstrate the event, and observations of this sort of outcome have rarely if ever been made in nature, although it is the usual thing in laboratory experiments. The events in succession might be considered as providing exceptions, since species are replaced during succession, but it is difficult to demonstrate that the replacement is due to competition. It has frequently been claimed that empty niches must abound in view of the ability of certain introduced species to succeed in establishing themselves. Such introductions, however, result in a decrease in numbers of some previously established species, as is shown dramatically in the history of oceanic islands. The author knows of no adequate data contrary to the generalization that successful introductions reduce the populations of one or more indigenous species. The implication that natural communities contain no unoccupied niches is clear.

The situation in an undisturbed natural community, then, illustrates the outcome of selection and interspecific competition. The species that are less successful in competition are not only less abundant, but are able to maintain populations only in restricted parts of the community to which

they are particularly well adapted. This accounts for the increasingly clumped distributions with decreasing abundance. Successful species are more numerous and occur throughout the communities to which they are well adapted, but the degree of success is not entirely uniform over the community, and we find that they are also clumped, but to a lesser degree than the rare species. Although the preceding sentences might be interpreted as indicating a sharp distinction between the two kinds of species, such is not the case. The continuous inverse relationship between clumping and abundance provides no validation for the concept that dominance and non-dominance are distinct and separable characteristics of the different species of soil arthropods studied. Hence, there is no justification other than convenience for omitting any species from an analysis of a community. The importance of knowing the relative abundance of the species is shown both in the demonstration that it provides a valid method of showing the amount of organization present and in the comparison between the 2 communities, where the same species assume very different degrees of importance. A mere statement of the presence of these species or even the frequency of occurrence in a given series of samples could easily lead to wrong conclusions about them.

Summary

The organization of natural communities was studied from the standpoint of the relative abundance of the species of microarthropods in the soil of 2 similar communities on a long-abandoned field. An examination of the details of distribution shows a continuous inverse relationship between abundance and clumping of the more than 100 species studied. This observation provides a basis for explaining why various empirically determined "indices of diversity" are not constant when increasingly large samples from the same community are analyzed. The strong clumping of the rare species means that with increased sampling new rare species are more likely to be added to the total than are additional specimens of rare species already recorded.

In spite of the dependence of the index of diversity on sample size, it can be used to show some interesting relationships, including a crude but completely objective separation of samples from similar communities. It is thus quite useful in situations such as plankton studies where there is no *a priori* separation of samples on the basis of the appearance of the area from which they came.

The most important use of data of this kind is in MacArthur's model based upon the biological hypothesis that the niches represented by different species abundances are contiguous but non-overlapping. This implies that food determines the abundance of all species, since it is the only factor that is completely utilized and cannot be shared by different species. MacArthur's assumption that the sizes of the niches conform to a random distribution is not confirmed. The departure from randomness is found to be greater with increased sample size as long as the samples come from the same community, but decreases if heterogeneous material is added in the form of samples from another community. These results indicate the degree of organization of the community, since, from information theory, it follows that organization is measured as departure from randomness. The organization of a community results from the outcome of interspecific competition for the available resources, and is expressed both in the relative abundance and the spatial distribution of the constituent species.

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References

Andrewartha, H. G. 1957. The use of conceptual models in population ecology. Cold Spring Harbor Symp. Quant Biol. **22**: 219-232.

Anscombe, F. J. 1948. The transformation of poisson, binomial, and negative binomial data. Biometrika **35**: 246-254.

———. 1949. The statistical analysis of insect counts based on the negative binomial distribution. Biometrics **5**: 165-173.

Arrhenius, O. 1921. Species and area. Jour. Ecol. **9**: 95-99.

Beauchamp, R. S. A., and **P. Ullyott.** 1932. Competitive relationships between certain species of freshwater triclads. Jour. Ecol. **20**: 200-208.

Blackith, R. E. 1958. Nearest-neighbor distance measurements for the estimation of animal populations. Ecology **39**: 147-150.

Bliss, C. I., and **D. W. Calhoun.** 1954. An outline of biometry. New Haven. Yale Cooperative Corp.

Bliss, C. I., and **R. A. Fisher.** 1953. Fitting the negative binomial distribution to biological data. Biometrics **9**: 176-200.

Brian, M. V. 1953. Species frequencies in random samples from animal populations. Jour. Anim. Ecol. **22**: 57-64.

Cain, S. A. 1938. The species-area curve. Amer. Midl. Nat. **19**: 573-581.

———, and **F. C. Evans.** 1952. The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich. **52**: 1-11.

Clark, P. J., and **F. C. Evans.** 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology **35**: 445-453.

Cole, L. C. 1946a. A study of the cryptozoa of an Illinois woodland. Ecol. Monogr. **16**: 49-86.

———. 1946b. A theory for analyzing contagiously distributed populations. Ecology **27**: 329-341.

Dice, L. R. 1952. Measure of spacing between individuals within a population. Contrib. Lab. Vert. Biol. Univ. Mich. **55**: 1-23.

Dixon, W. J., and **F. J. Massey, Jr.** 1951. Introduction to statistical analysis. New York. McGraw-Hill.

Evans, F. C., and **S. A. Cain.** 1952. Preliminary studies on the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich. **51**: 1-17.

Fisher, R. A., A. S. Corbet, and **C. B. Williams.** 1943. The relation between the number of species and the number of individuals in a random sample from an animal population. Jour. Anim. Ecol. **12**: 42-58.

Gleason, H. A. 1920. The applications of the quadrat method. Bull. Torrey Bot. Club **44**: 463-481.

———. 1922. On the relation between species and area. Ecology **3**: 158-162.

———. 1929. The significance of Raunkiaer's law of frequency. Ecology **10**: 406-408.

Hairston, N. G. 1951. Interspecies competition and its probable influence upon the vertical distribution of Appalachian salamanders of the genus Plethodon. Ecology **32**: 266-274.

———, and **G. W. Byers.** 1954. The soil arthropods of a field in southern Michigan. A study in community ecology. Contrib. Lab. Vert. Biol. Univ. Mich. **64**: 1-37.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. **22**: 415-427.

Kenoyer, L. A. 1927. A study of Raunkiaer's law of frequence. Ecology **8**: 341-349.

Kontkanen, P. 1957. On the delimitation of communities in research on animal biocoenotics. Cold Spring Harbor Symp. Quant. Biol. **22**: 373-375.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**: 399-417.

MacArthur, R. H. 1957. On the relative abundance of bird species. Proc. Nat. Acad. Sci. U. S. **43**: 293-295.

Macfadyen, A. 1954. The invertebrate fauna of Jan Mayen Island (East Greenland). Jour. Anim. Ecol. **23**: 261-297.

———. 1957. Animal Ecology. Aims and Methods. London. Sir Isaac Pitman and Sons, Ltd.

Margalef, R. 1951. Diversidad de especies en las comunidades naturales. P. Inst. Biol. Apl. **9**: 5-27.

———. 1956. Informacion y diversidad espicifica en las cominudades de organismos. Inv. Pesq. **3**: 99-106.

———. 1957. La teoria de la informacion en ecologia. Mem. Real Acad. Ciencias y Artes de Barcelona **32**: 373-449.

Neyman, J. 1939. On a new class of "contagious" distributions, applicable in entomology and bacteriology. Ann. Math. Stat. **10**: 35-57.

Numata, M. 1950. The homogeneity of plant communities—Studies on the structure of plant communities VI. Bot. Mag. (Tokyo) **63**: 203-309.

Preston, F. W. 1948. The commonness, and rarity, of species. Ecology **29**: 254-283.

Raunkiaer, C. 1909. Formationsundersögelse og Formationsstatistik. Bot. Tidsske. **30**: 20-132.

———. 1918. Recherches statistiques sur les formations vegetales. Det. Kgl. Danske Videnskabens Selskab. Biol. Meddel. **1**: 1-80.

———. 1934. The life forms of plants and statistical plant geography. Oxford. Clarendon Press.

Romell, L. G. 1930. Comments on Raunkiaer's and similar methods of vegetation analysis and the law of frequency. Ecology **11**: 589-596.

Shinozaki, K. 1955. Several problems on the law of geometrical progression. Physiology and Ecology **6**: 127-144.

———, and **N. Urata.** 1953. Apparent abundance of different species. Res. Pop. Ecol. **2**: 8-21.

Thomas, M. 1949. A generalization of Poisson's binomial limit for use in ecology. Biometrika **36**: 18-25.

Thompson, H. R. 1956. Distribution of distance to Nth neighbor in a population of randomly distributed individuals. Ecology **37**: 391-394.

Thomson, G. W. 1952. Measures of plant aggregation based on contagious distributions. Contrib. Lab. Vert. Biol. Univ. Mich. **53**: 1-17.

Whittaker, R. H., and **C. W. Fairbanks.** 1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecology **39**: 46-65.

Williams, C. B. 1944. Some applications of the logarithmic series and the index of diversity to ecological problems. Jour. Ecol. **32**: 1-44.

———. 1947a. The generic relations of species in small ecological communities. Jour. Anim. Ecol. **16**: 11-18.

———. 1947b. The logarithmic series and its application to biological problems. Jour. Ecol. **34**: 253-272

———. 1953. The relative abundance of different species in a wild animal population. Jour. Anim. Ecol. **22**: 14-31.

SMALL MAMMALS IN OLD FIELD SUCCESSION

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INTRODUCTION

Mammalian population changes accompanying vegetational succession have been studied in various parts of the country. In the mid-west, Smith (1940) and Beckwith (1954) included mammals in their study of vegetational succession on abandoned farmlands. Aldrich (1943) and Gunderson (1950) correlated occurrence of mammals with vegetational succession in bogs. In Illinois Verts (1957) examined small mammal succession in upland strip mines, while Wetzel (1958) studied mammalian succession for a period of nineteen years on the floodplains.

In the south and southeast, recent work on plant succession has been done by Oosting (1942), Keever (1950) and Bard (1952). Byrd (1956) studied farm game in relation to ecological succession in Virginia, while Gentry and Odum (1957) examined small rodent populations in old fields in Georgia.

Except for Dalke's (1942) work with the cottontail rabbits in Connecticut little information is available on the relationship of small mammals to old field succession in New England. Most of the work in this region has emphasized the silvicultural and vegetational aspects of succession (Lutz 1928, Bromley 1935, Raup 1940).

The purposes of this study were to examine small mammal populations in upland old field successional stages in New England during the different seasons in one year and to evaluate biotic and other environmental factors in the successional series that affect these populations.

I am indebted to Dr. Ralph M. Wetzel, Zoology Department, University of Connecticut, for his guidance throughout this study and to both Dr. Ralph M. Wetzel and Dr. James N. Layne, Department of Biology, University of Florida, for helpful suggestions after critically reading the manuscript.

DESCRIPTION OF STUDY AREA

The area selected for this study is located approximately 3 miles S. W. of the University of Connecticut campus at Storrs, Connecticut. The areas were three adjacent seral stages characteristic of upland secondary succession in southern New England. The age since abandonment of each area was determined by interviews with the owners and neighbors, estimates of professional foresters, and tree ring counts. The age since abandonment and size of each area is as follows: pioneer stage (Area 1) was 8 to 10 years old and 4.2 acres (Figure 1); midseral stage (Area 2)

FIG. 1. Area 1 in the summer. Most of the small mammal captures were from the ends of the trap lines which extended into the more dense vegetation.

FIG. 2. Area 2 in the summer. Typical view of the habitat where 42% of all Peromyscus were trapped.

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was 24 to 28 years old and 7.6 acres (Figure 2); mature woodland (Area 3) was 60 to 80 years old and 8.8 acres (Figure 3).

FIG. 3. Area 3 in the summer.

The study area borders on a transition zone between the central hardwood forests and the northern hardwood forest regions of the United States as described by Westveld, *et al.* (1956). Chestnut was an important forest component in former days, but makes up only a small part of the forest now. Without exception, every chestnut in the study area was infected with the chestnut blight disease, *Endothia parasitica.*

Almost all the land in the region has been farmed or cleared at least once. According to Bromley (1935) "between 1820 and 1850, the total area of cleared land in southern New England was 75 to 80%." Since then there has been a gradual abandonment of farm lands and a slow succession to the oak-hickory forest.

Topography and Soils

The present topography is the result of a melting down of a stagnant glacier some 19,500 years ago (Flint 1930, Urry 1948). Rolling hills dissected by streams are prominent features of the landscape today. Elevation of the study area was 620 feet. There was a 3 to 8% N. W. slope and little or no significant water or wind erosion on any area. The ecotone between Areas 1 and 3 was moderately well drained with a 0 to 3% slope. The soils of the study area were of the Brown Podzol type characteristic of much of northeastern United States. The soils in the 3 seral stages studied were of the Charlton series which are characterized by a loamy texture, being derived from mica and schist, and containing some stone fragments. In the ecotone the soil was of the Sutton series and the soil profile characterized by mottling.

Vegetation

The area was sampled by a straight line transect parallel to the lines of traps through each area. Each species in the shrub and tree strata was identified and tabulated and the frequency of the grasses and herbs was estimated. Relative abundance of these plants was expressed in terms of the frequency index developed by Lutz (1928). These data are summarized in Table I. The frequency indices employed with percentages for each are as follows: 1 (0-20%), 2 (20-40%), 3 (40-60%), 4 (60-80%), 5 (80-100%). Botanical nomenclature is from Fernald (1950).

In old field succession in the Northeast, various annual and biennial species are abundant during the first few years after abandonment. Later, the perennial grasses become dominant and the field is invaded by eastern red cedar, *Juniperus virginiana* L. In the pioneer stage, fescue, *Festuca rubra* L. and Kentucky blue grass, *Poa pratensis* L. were the dominants in the herb layer while smooth sumac, *Rhus glabra* L. and field juniper, *Juniperus communis* L. were the dominant shrubs and *Juniperus virginia* was the dominant tree. Most of the trees and shrubs were in small clumps on the edge and were just beginning to spread into the center of the field. While their frequency is indicated as 1 (0-20%) in Table I, most of the frequencies of the woody plants fell below 10%.

The midseral stage was characterized by a dense undergrowth of *Juniperus communis,* which indicated heavy grazing in earlier days, and with a dense, uniform stand of birches, *Betula* sp. The height of the canopy was approximately 30 feet. The ececis of some species of oak and hickory in this stage are the predecessors of the next association.

The third seral stage was a mesophytic oak-hickory association. The height of the canopy averaged 75 feet. In this habitat the herbaceous and grass growth of the 2 preceding seral stages was almost non-existent and a humus layer ranging from ¼ to 1" in depth had developed. Although the author was not aware of any old, undisturbed forests in the general area of the study that could serve as direct evidence of the upland climax typical of the region, the presence of young beech and maples suggests a beech-maple climax community. No hemlocks, even as seedlings were present.

TABLE I. Vegetation of study areas. Diameter breast height indicated within parentheses. f = frequency: Index explained in test

AREA 1 Abandoned pasture age 8-10 years: 1.7 Hectares (4.2 acres)		AREA 2 Forest edge pasture age 24-28 years: 3.1 Hectares (7.6 acres)		AREA 3 Forested pasture age 60-80 years: 3.6 Hectares (8.8 acres)	
GRASSES AND HERBS	f	GRASSES AND HERBS	f	GRASSES AND HERBS	f
Agropyron repens	2	Agropyron repens	1	Lycopodium complanatum	1
Agrostis tenuis	1	Aster nova-belgi	1	Lycopodium obscurum	1
Aster nova-belgi	1	Dactylis glomerata	1	Polystichum acrostichoides	1
Dactylis glomerata	3	Danthonia spicata	1		
Danthonia spicata	1	Festuca rubra	1	SHRUBS	
Festuca ovina	1	Lycopodium obscurum	2	Aronia melanocarpa	1
Festuca rubra	4			Corylus americana	1
Panicum lanuginosum	1	SHRUBS		Kalmia latifolia	1
Phleum pratense	1	Corylus americana	1	Vaccirium corymbosum	2
Poa pratensis	4	Juniperus communis	4	Vibernum acerifolium	3
Polytrichum commune	1	Vaccinium corymbosum	1		
Rosa rugosa	1			TREES	
Rubus sp.	1	TREES		Acer rubrum	(3.1)1
Rubus flagellaris	1	Betula allegheniensis	(3.1)3	Acer saccharum	(2.7)1
Solidago sp.	1	Betula lenta	(3.3)3	Amelanchier sp.	(.2)1
Spiraea tomentosa	1	Betula populifolia	(4.6)4	Betula populifolia	(3.0)1
		Carpinus carolinianus	(1.0)1	Carya glabra	(3.8)3
SHRUBS		Carya glabra	(2.9)1	Carya ovata	(4.0)2
Juniperus communis	2	Carya ovata	(1.2)1	Carpinus caroliniana	(.4)2
Myrica pennsylvanica	1	Cornus florida	(.5)1	Castanea dentata	(2.1)1
Rhus glabra	2	Fraximus americana	(2.7)1	Fagus grandifolia	(3.1)1
		Juniperus virginiana	(4.0)1	Ostrya virginiana	(1.4)1
TREES		Quercus alba	(4.0)1	Prunus virginiana	(.4)1
Acer rubrum	(1.2)1	Quercus velutina	(4.1)1	Prunus serotina	(1.0)1
Betula nigra	(2.6)1			Quercus alba	(9.5)4
Betula populifolia	(1.4)1			Quercus rubra	(8.0)3
Fraximus americana	(2.0)1			Quercus velutina	(14.5)5
Juniperus virginiana	(2.1)1			Sassafras albidum	(.3)1
Prunus virginiana	(.5)1				

The ecotone between the field and the forest had its own characteristic vegetation. The ecotone had an area of 3.8 acres and was rectangular in shape. *Festuca rubra* was the dominant herb and *Juniperus communis* and alder, *Alnus incana* (L.), were the dominant shrubs in this habitat. The principal tree species were *Betula populifolia* Marsh and *Juniperus virginiana*.

Climate

The climate of the region is characterized by long, cool winters and short, warm summers. The following climatological data were recorded during the trapping period for each seral stage: general weather conditions, cloud cover the night before and during the day, 2" sub-surface temperature, soil surface temperature, air temperature at 5 foot level, and dry and wet bulb temperatures. The dew point, relative humidity, and vapor pressure were also determined. Observations and measurements were made between 8:00 and 9:00 a.m. during the period between September and May and between 9:00 and 10:00 a.m. in the months June through August. The method of determining cloud cover was that of Haynes (1947) in which the percentage of clouds compared to the clear sky is estimated in each of 4 quadrants and the mean taken. These determinations were made between 8:30 and 9:30 p.m.

Figure 4 is a climograph of the 3 seral stages and compares the morning surface temperature with relative humidity. The soil surface temperature, rather than air temperature, was chosen for comparison since recent work indicates that this is the temperature most affecting behavior of small mammals (Bodenheimer 1941, Stinson and Fisher 1953).

The differences in microclimate in the 3 areas are more extreme during the warm than during the cold season. Figure 4 shows that the relative humidity and soil surface temperatures were similar in all 3 habitats during the winter months of November through March. The morning relative humidity remained between 77 and 87% and the thermostatic effect of snow prevented any extreme soil surface differences. However, there was a pronounced dry to moist gradient from pioneer to forest stages during the months of April through October.

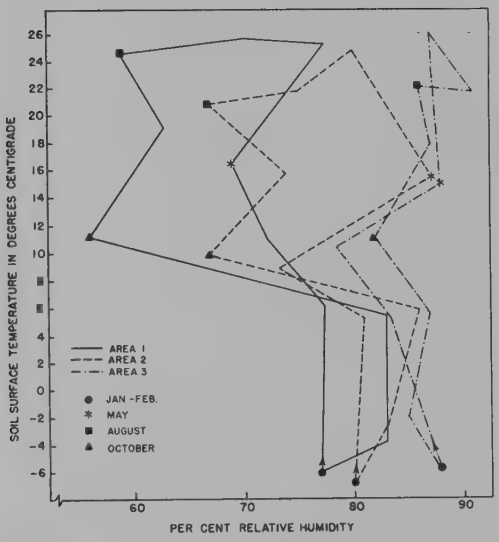

FIG. 4. A climograph of 3 seral stages of old field succession in Connecticut. Months not designated by symbols follow chronologically in the direction of the arrow.

METHOD OF STUDY

Live trapping using Sherman live traps 3" × 3" × 10" was employed for 10 consecutive days each month for one year (April, 1957 to March, 1958) with the following 2 exceptions: the traps were set for 6 days in April, 1957 and, because of snowfall, the January-February, 1958 trapping period was combined for 10 days from January 29 to February 7. The total number of trap nights was 6996. Intervals between trapping periods averaged 23 days, with a range of from 11 to 48 days. The bait consisted of sun-flower seeds and peanut butter. The entire study area was trapped simultaneously by means of 22 traps in 2 parallel lines in each habitat. The distance between traps and the 2 lines was 42 feet. The trap lines were placed at least 300 feet inward from the edge of adjacent habitats or any physical boundary. According to Dice (1941) "traplines of measured length, maintained for a standard number of days should give samples of the population that are comparable for different types of habitats, different seasons and different areas." Live-trapped animals were marked by toe clipping and ear punching.

On March 29, 1958, snap traps were put out in the same pattern as live traps in all 3 seral stages. In addition, the ecotone between the field and forest was snap trapped, employing the same pattern as the other areas. Trapping was continued for 7 days. At the end of this snap trapping period, 8 bucket traps containing 3 inches of water were put out for a 10 day period. Four were placed in the field and 4 in the ecotone. These pails were buried in possible runways in the same line as snap traps and checked daily. The snap and bucket trapping at the beginning of the spring breeding season furnished checks by alternate methods of results obtained the preceding year as follows: (1) completeness of sampling of species in the habitats (2) distribution, particularly in ecotone or intergrading areas between established quadrats and (3) reliability of density estimates.

RESULTS

Peromyscus leucopus noveboracensis (Say)

The total numbers of white footed mice captured during the period of study in areas 1, 2, and 3 were 56, 118, and 89 respectively. The frequency with which mice were taken in the three seral stages differs significantly from a 1:1:1 ratio ($\chi^2 = 21.9$) ($P < .01$) and indicates the highest overall population density in the midseral stage. This tendency was evident at all seasons of the year. These data suggest a 2:4:3 occurrence of *Peromyscus* in this sere.

Population estimates

Population densities of *Peromyscus* were estimated in the following ways (Table II): (1) trap nights necessary to catch one mouse (2) number of mice per parallel trap lines (3) number of mice per acre and (4) the time-relative population.

The number of trap nights necessary to capture one individual in each seral stage throughout the year (modified from Grinnell 1914) is based on a total of 220 trap nights for each habitat in each trapping month (except 132 for each in April) and a yearly total of 6996 trap nights.

The number of mice per parallel trap lines are given in terms of average number of *Peromyscus* caught on two 462 foot trap lines (separated 42 feet) per night, throughout a 10 day trapping period.

The method of computing the number of mice per acre was adopted from Dice (1938). Considering the traveling distances found in this study and analyzing home range data of Stickel (1948) it was decided to use 100 and 70 feet as the average radii of traveling distances of *Peromyscus* in New England from May to September and from October to April respectively. Then, the number of individuals in contact with the traps was estimated by assuming that the lines will draw from an area equal to the mean traveling radius of the

TABLE II. Population estimates and comparative densities of Peromyscus throughout one year on three typical stages of old field succession in New England

Trapping period	Area	Trap nights per mouse	Mice per parallel trap lines	Mice per acre	Time rel. pop. in %
April 13-18	1	66	.3	1.1	.....
	2	12	1.9	5.8	.....
	3	16	1.2	3.7	.....
May 2-11	1	27	.8	3.1	+15.2
	2	22	1.0	3.9	− 1.1
	3	31	.7	2.7	0.0
June 9-18	1	22	1.0	3.1	+ .3
	2	10	2.1	8.1	+ 4.2
	3	12	1.8	6.9	+ 4.1
July 1-10	1	20	1.1	4.2	+ .5
	2	13	1.6	6.2	− 1.1
	3	13	1.7	6.6	− .3
Aug. 7-16	1	55	.4	1.5	− 1.7
	2	11	2.0	7.7	+ .6
	3	13	1.6	6.2	0.0
Sept. 1-10	1	55	.4	1.5	− 2.0
	2	15	1.4	5.4	− .8
	3	22	1.0	3.1	− 1.6
Oct. 1-10	1	22	1.0	5.3	+13.3
	2	20	1.1	5.8	− 1.0
	3	31	.6	3.2	− 1.3
Nov. 11-20	1	110	.2	1.1	− 1.9
	2	31	.6	3.2	− 1.1
	3	44	.5	2.6	− .4
Dec. 2-11	1	110	.2	1.1	0.0
	2	27	.8	4.2	+ 1.5
	3	220	.1	.5	− 3.8
Jan.-Feb. 29-7	1	73	.3	1.5	+ .8
	2	220	.1	.5	− 1.5
	3	220	.1	.5	0.0
March 9-18	1	110	.2	1.1	− .8
	2	44	.5	2.6	+10.2
	3	73	.3	1.6	+ 5.1

animal. On this basis, the trap lines sampled from 2.6 and 1.9 acres respectively.

The time-relative population data are obtained from a modified use of the mean annual growth formula (Allee *et al.* 1949, p. 266). The figures represent the average rate of change in size of the *Peromyscus* population between trapping periods relative to the population of the last day of trapping in the preceding month. The population of the following month is also taken as that of the last day of trapping.

These various methods of presenting the data show that the population build-up and decline is quite rapid in the spring and early fall. White footed mice were most readily captured in the summer months. The midseral stage required less trap nights per *Peromyscus* than any other seral stage throughout the year. There was a gradual decline from the high populations in the summer months to a low in January-February. The densities of 5 to 8 per acre in the summer and fall are in close agreement with work of other investigators in similar type habitats (Burt 1940, Hanson 1944, Stickel 1948).

The population of immatures reaches its peak at the latter part of June. The peak in the adult population is in the latter part of August in the last 2 seral stages and in October in the pioneer stage.

Recaptures

Of the 263 *Peromyscus* live trapped, marked and released, only 40% were recaptured. Very few recaptures were made from November through February while 60% of the recaptures were made during the 3 months of June, July and August. The largest number of individual recaptures was 8 for one female in the midseral stage and for one male in the forest stage over the period from April to June. The longest time between recaptures (September-March) was for an adult female in Area 2. At no time was an animal recaptured outside the area in which it was marked.

Breeding season

The immatures were identified by their smaller size and gray color. The sub-adults (not breeding but with some brown streaks of adults) were classified as immature.

The first captures of immature *Peromyscus* in the spring were a female on May 7 in the field, two females on May 8 and 10 in the midseral stage, and one male on June 9 in the woodland. Immatures last taken in the fall were a male and female on October 5 in the field, a male and female on October 6 in the midseral stage, and a female on October 2 in the woodland.

The young represent approximately 50% of the sample population in June. From July through September the number of young represent 15 to 20% of the catch. A second peak of immatures in all 3 areas occurred in October, when the number of young represented 20 to 33% of the population. At no time during the study did the number of immatures account for more than 52% of the monthly sample in any habitat.

The first pregnant females in areas 1, 2, and 3 were captured on April 15, 15, and 18 respectively. More pregnant females were captured in May than any other month. The last pregnant females in the 3 areas were caught on October 6, October 3, and September 7 respectively.

Combining these data with some obtained from

Svihla (1932, 1935) on the length of gestation and age at weaning, the breeding season in New England then, extends from the middle of March to the beginning of October.

Sex ratios

A total of 148 males and 115 females was taken in all areas during the study, giving an overall sex ratio of 56% males to 44% females. The percentages of males in the pioneer, midseral, and woodland stages were 54, 60, and 58% respectively. The male sex ratios during the non-breeding season (October-March) and breeding period (April-September) were 41 and 60% in the field, 54 and 62% in the midsere, and 47 and 60% in the oak-hickory woodland. The differences in sex ratios during the breeding season in all seral stages were significantly different from 1 ♂ :1 ♀ at the 1% level.

The larger proportion of males during the breeding season is probably to be explained on the basis that pregnant females were less active and that the males roam more at this season of the year.

Longevity and mortality

The estimated longevity of *Peromyscus,* based on the average time that 263 individuals were in the areas and, assuming that the young leave the nest at a mean age of 25 days, was $4.06 \pm .06$ months. Blair (1948) using similar techniques, found a life span of $4.60 \pm .21$ months in Michigan for the same species. An adult male was found dead on the surface of the ground on November 18, 1957, and another on March 15, 1958. In both cases there had been a sudden drop of 14 to 16°C in soil surface temperature.

Although no direct evidence for *Blarina* predation on *Peromyscus* was obtained, a correlation was apparent between the peak of shrew population in July and a decline in the total number of *Peromyscus* at the same time, although other factors such as bait responses may have been involved.

Differential movements

The distances between release and recaptures are referred to as traveling distances. Although distances between recapture in this study are not meant to signify home ranges, it is worthwhile to note that Dice (1941) reported "size of home ranges differ for males, females and young and at different times of the year."

The average distances traveled by adult males in the pioneer to woodland stages were 92, 74, and 105 feet respectively. Corresponding values for adult females were 71, 70, and 83 feet respectively. It is interesting to note that the average distances traveled by females in all habitats were nearly equal, while the males of the woodland area moved more extensively than males of the other two seral stages. In Area 2, where 42% of the *Peromyscus* were caught, males and females showed approximately the same traveling distances.

During the time of highest population density (May through November) it was observed that males were continually recaptured at much more distant points than were females. The traveling distances of males and females in all habitats were analyzed and, testing the frequency distribution by Chi-square in categories of male and female and over and less than 100 feet, the result was $\chi^2 = 5.28$ (1 d. f.) (P. = .02). Pearson (1953) found similar travel differences between the sexes of *P. gossypinus* in Florida.

The greatest average traveling distance for any month was 210 feet for adult males in Area 3 in April. This was probably due to the oncoming breeding season. The smallest traveling distance was an average of 30 feet for adult males in the midseral stage in November. The longest distance between an individual recapture was 378 feet in the case of an adult male in the woodland in July.

The traveling distances of immatures were calculated separately for the interval from June to October. The mean traveling distances of male and females in the three areas from pioneer to woodland stages were 36′ ♂ 34′ ♀, 114′ ♂ 97′ ♀, and 85′ ♂ 64′ ♀ respectively. The greater traveling distances of immatures compared to adults in the midseral stage is believed to be due to competition produced by the high resident population already established.

Various authors have found decreased activity of *Peromyscus* in the winter (Hatfield 1940, Hamilton 1941, Thomsen 1945, Sealander 1952). This behavior of *Peromyscus* in winter would tend to reduce traveling distances, which I have found to be the case in all habitats. Under these conditions, the low point in the population (January-February), based on my trapping results, might be due to the storing of food and the sedentary habits of the mice.

Seasonal occurrence of bot fly larvae

In September and October the rodent bot fly larvae, *Cuterebra fontinella* Clark, was found infecting *Peromyscus*. The first mouse carrying a bot fly larva was caught September 3 in the midseral stage. Approximately 38% of the mice caught during the month were parasitized, and 19% of the mice taken October 1-4 were infected. No infected mice were taken after the latter date.

All infected mice were captured in Area 2 except 2 in Area 3. In all cases the larvae were located in the genital region. Two mice had 2 larvae each while the remainder had only a single larva. It was noted that infected mice were more lethargic when taken out of the traps and more easily handled.

Weather and activity

Few investigators have attempted to correlate the amount of cloud cover with the amount of activity in small rodents. Blair (1951), Youngman (1956), and Gentry and Odum (1957) have found decreased activity among small mammals on clear, moonlight nights. Similar results were obtained in this study. Activity of *Peromyscus* and degree of cloudiness the night before capture were analyzed from June to October. A total of 50 nights (3300 trap nights) of trapping was involved. The number of captures, both new and recaptures, was used as an index of activity and the data for all habitats were combined. A correlation coefficient of $r = +.74$ ($P < .01$) between activity and sky cover was obtained, which indicates that *Peromyscus* was more active as the degree of cloudiness increased. No difference was observed between amount of leaf canopy and activity.

The data from June to September suggested a correlation between rainfall and activity. When rain fell in the evening before midnight, the number of mice found in the traps the following day was significantly less than on days when rain did not fall the preceding night. Rain after midnight, however, did not significantly change the number of mice found in the traps the next day. This would suggest the peak of activity of *Peromyscus* occurs in the evening.

Blarina brevicauda talpoides (Grappes)

A total of 41 short tailed shrews was caught during the year of live trapping. Twenty-one were caught in the midseral stage and 13 in the oak forest. Despite the fact that the traps were checked as early as possible in the morning, 14 of the *Blarina* were found dead and only 2 of those marked and released were subsequently recaptured. Both were retaken in the same 10 day trapping period in July.

Although the short-tailed shrews were captured throughout the year, 2 peaks in numbers, July and October, were particularly noticeable. In all, 18 were caught in July and 11 in October in all habitats combined. Of the 22 captured in the midseral stage, 9 were males and 13 females. Of the 12 captured in the oak woodland, 6 were male and 6 female. Three males and 4 females were taken in the pioneer stage. These data indicate a slight preponderance of females in the various habitats. The abundance of *Blarina* in the summer months agrees with other investigations showing a peak of breeding activity in the spring and fall and a period of low breeding activity during the warm, summer months (Hamilton 1929, Blair 1940).

As in the case of *Peromyscus,* the short-tailed shrew was most abundant in the midseral stage. This was probably the result of the abundant cover and protection offered by the thick undergrowth. The ratio of 2:5:3 occurrence of *Blarina* in Areas 1, 2, and 3 respectively was found to differ significantly from 1:1:1 at the 1% level. This ratio was also evident at all seasons of the year. Beckwith (1954), in Michigan, found *Peromyscus leucopus* and *Blarina brevicauda* the most common species on farmlands that had been abandoned from 16 to 25 years.

Other Mammals

In addition to the white footed mouse and short-tailed shrew, other mammals were recorded on the study area through live trapping, snap trapping, bucket trapping and visual observations.

Three eastern moles, *Scalopus aquaticus* (L.), 4 house mice, *Mus musculus* L. and two Norway rats, *Rattus norvegicus* (Berkenhout) were found in the pioneer stage. The latter 2 species were captured only in the vicinity of an abandoned farmhouse adjacent to the study area. Twelve New England cottontails, *Sylvilagus transitionalis* (Bangs) were observed at the borders of the field and in the ecotone. Woodchucks, *Marmota monax* (L.) were observed in all seral stages but were most common in the pioneer and midseral stages. In agreement with Wetzel (1958), the woodchucks in the woodland were most prevalent in sites where the tree canopy was not completely closed. Eighteen red-backed voles, *Clethrionomys gapperi* (Vigors), were trapped in all seral stages combined, but 14 were found in the midseral stage. *Clethrionomys* was most common in December in Area 2 where it represented 27% of the total catch of all mammals. Mammals observed or trapped exclusively in the forest were 16 chipmunks, *Tamias striatus* (L), 15 gray squirrels, *Sciurus carolinensis* Gmelin, and 4 red squirrels *Tamiasciurus hudsonicus* (Erxleben). The chipmunk was most common in September when 10 were trapped.

The masked shrew, *Sorex cinereus* Kerr, was taken for the first time during snap trapping in April 1958. Eight of these shrews were caught in the midseral stage and 3 in the woodland. Specimens were taken in snaptraps in sites where

live traps had been placed each month during the preceding year.

Animals which were sighted or trapped only once included the red fox, *Vulpes fulva* (Desmarest), gray fox, *Urocyon cinereoargenteus* (Schreber), and woodland jumping mouse, *Napeozapus insignis* (Miller), in the midseral habitat; the long-tailed weasel, *Mustela frenata* Lichtenstein, in the last two seral stages; and the skunk, *Mephitis mephitis* (Schreber), and opossum, *Didelphis marsupialis* L., in the oak woodland.

Summary

1. Ecological succession was studied for one year on 3 adjacent old farm fields with similar slope and soil profiles, but differing in age since abandonment from approximately 8 to 80 years.

2. The successional pattern was from pasture grass and herbs through shrubs such as sumac, *Rhus glabra,* and field juniper, *Juniperus communis,* and low trees such as red cedar, *Juniperus virginiana,* and various birches, *Betula* spp. to a closed canopy, 80 year old oak-hickory forest.

3. The microclimate of the sere was found to be relatively similar during the winter months, but differed in showing a distinct dry to moist gradient from pioneer to woodland seral stages in the spring, summer, and fall months.

4. Live trapping employing the same length of lines and equal number of traps was carried on in each area 10 days each month for one year. This was followed by snap and bucket trapping.

5. The total numbers of most mammals, in this sere, increased up to the midseral stage and declined slightly in the woodland. This was correlated with modifying effects of the changing vegetation in the breeding season.

6. Two hundred sixty-three *Peromyscus leucopus noveboracensis* and 41 *Blarina brevicauda talpoides* were live trapped in 6996 trap nights. The statistically significant ratios of occurrence of *Peromyscus* and *Blarina* in the 3 stages of old field succession were 2:4:3 and 2:5:3 respectively. Both mammals were most common in the summer months.

7. The breeding season of *Peromyscus* extended from March to October and sex ratios were significantly different at this time. Significant correlations were found between activity of *Peromyscus* and degree of cloud cover and time of rainfall at night. Traveling distances were correlated with age, sex, habitat, and season of the year.

References

Aldrich, J. W. 1943. Biological survey of the bogs and swamps in northeastern Ohio. Amer. Mid. Nat. **30**: 346-402.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and **K. P. Schmidt.** 1949. Principles of Animal Ecology. Philadelphia, W. B. Saunders Co.

Bard, G. E. 1952. Secondary succession on the Piedmont of New Jersey. Ecol. Monog. **22**: 195-215.

Beckwith, S. L. 1954. Ecological succession on abandoned farm lands and its relationship to wildlife management. Ecol. Monog. **24**: 349-375.

Blair, W. F. 1940. Notes on home ranges and populations of the short-tailed shrew. Ecology **21**: 284-288.

———. 1948. Population density, life span, and mortality rates of small mammals in the blue-grass meadow and blue-grass field associations of southern Michigan. Amer. Mid. Nat. **40**: 395-419.

———. 1951. Population structure, social behavior, and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus leucocephalus*). Contr. Lab. Vert. Biol. Univ. Mich. **48**: 1-47.

Bodenheimer, F. S. 1941. Observations on rodents in Herter's temperature gradient. Physiol. Zool. **14**: 186-192.

Bromley, S. W. 1935. The original forest types of southern New England. Ecol. Monog. **5**: 61-89.

Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool. Univ. Mich. **45**: 1-58.

Byrd, M. A. 1956. Relation of ecological succession to farm game in Cumberland County in the Virginia Piedmont. Jour. Wildl. Mgt. **20**: 188-195.

Dalke, P. D. 1942. The cottontail rabbits in Connecticut. State Geol. and Nat. History Survey Bull. **65**; Hartford.

Dice, L. R. 1938. Some census methods for mammals. Jour. Wildl. Mgt. **2**: 119-130.

———. 1941. Methods for estimating populations of mammals. Jour. Wildl. Mgt. **5**: 398-407.

Fernald, M. L. 1950. Gray's Manual of Botany. Eighth Edition. New York, American Book Co.

Flint, R. F. 1930. The Glacial Geology of Connecticut. State Geol. and Nat. History Survey Bull. **47**: Hartford.

Gentry, J. B. and **E. P. Odum.** 1957. The effect of weather on the winter activity of old field rodents. Jour. Mamm. **38**: 72-77.

Grinnell, J. 1914. An account of the mammals and birds of the Lower Colorado Valley. Calif. Univ. Publ. in Zool. **12**: 51-294.

Gunderson, H. L. 1950. A study of some small mammal populations at Cedar Creek Forest, Anoka County, Minnesota. Minn. Mus. Nat. Hist. Univ. Minn. Publ. No. 4.

Hamilton, W. J., Jr. 1929. Breeding habits of the short-tailed shrew, *Blarina brevicauda*. Jour. Mamm. **10**: 125-135.

———. 1941. The food of small forest mammals in eastern United States. Jour. Mamm. **22**: 250-263.

Hanson, H. C. 1944. Small mammal censuses near Prairie du Sac, Wisconsin. Trans. Wisconsin Acad Sci. Arts and Letters **36**: 105-129.

Hatfield, D. 1940. Activities and food consumption in *Microtus* and *Peromyscus*. Jour. Mamm. **21**: 29-36.

Haynes, B. C. 1947. Techniques of Observing the Weather. New York, John Wiley & Sons.

Keever, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. Ecol. Monog. **20**: 229-250.

Lutz, H. J. 1928. Trends and silvicultural significance of upland forest succession in southern New England. Yale Univ. School Forestry Bull. 22.

Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. Amer. Mid. Nat. **28**: 1-126.

Pearson, P. G. 1953. A field study of *Peromyscus* populations in Gulf Hammock, Florida. Ecology **34**: 199-207.

Raup, H. M. 1940. Old field forests of southern New England. Jour. Arnold Arboretum **21**: 266-273.

Sealander, J. A., Jr. 1952. The relationship of nest protection and huddling to survival of *Peromyscus* at low temperature. Ecology **33**: 63-71.

Smith, C. C. 1940. Biotic and physiographic succession on abandoned eroded farmland. Ecol. Monog. **10**: 421-484.

Stickel, L. F. 1948. The trap line as a measure of small mammal populations. Jour. Wildl. Mgt. **12**: 153-161.

Stinson, R. H. and **K. C. Fisher.** 1953. Temperature selection in deer mice. Canadian Jour. Zool. **31**: 404-416.

Svihla, A. 1932. A comparative life history study of the mice of the Genus *Peromyscus*. Univ. Mich. Mus. Zool. Misc. Publ. No. 24: 1-39.

———. 1935. Development and growth of the prairie deermouse, *Peromyscus maniculatus bairdii*. Jour. Mamm. **16**: 109-115.

Thomsen, H. D. 1945. The winter habits of the northern white-footed mouse. Jour. Mamm. **26**: 138-141.

Urry, W. D. 1948. The radium content of varved clay and a possible age of the Hartford, Conn. deposits. Amer. Jour. of Science **246**: 689-700.

Verts, B. J. 1957. The population and distribution of two species of *Peromyscus* on some Illinois strip-mined land. Jour. Mamm. **38**: 53-59.

Westveld, M. *et al.* 1956. Natural forest vegetation zones of New England. Jour. Forestry **54**: 332-338.

Wetzel, R. M. 1958. Mammalian succession on midwestern floodplains. Ecology **39**: 262-271.

Youngman, P. M. 1956. Ecology of the striped field mouse in Korea. Jour. Mamm. **37**: 1-10.

COMPUTATION OF PRODUCTION FOR POPULATIONS OF AQUATIC MIDGE LARVAE[1]

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INTRODUCTION

Much information has accumulated on the bulk and composition of the benthic communities of lakes, but estimates of the rates of production of organic matter in such communities are generally missing from the literature. The various difficulties that one encounters in trying to make such estimates are well-known and sometimes almost insuperable. On the other hand, many of the species of benthic insects, here primarily Diptera in the family Chironomidae (Tendipedidae[3]), have life-cycles in which a given generation of larvae consists of individuals all of which have hatched at approximately the same time and all of which will emerge from the lake together. A lake's entire population of larvae belonging to such species will ordinarily be made up of a single age-class or of a very small number of distinguishable age-classes; under these circumstances the computation of rates of production for a single species becomes somewhat less difficult than it would be for a population with a more complicated age-distribution. Fortunately, larvae of such insects often contribute heavily to the total mass of a lake-bottom community, thus probably also to its total productivity.

Estimates of rates of production for populations of larvae of various chironomids appear in papers of Lundbeck (1926; North German Lakes), Borutzky (1939; Lake Beloje) and Anderson and Hooper (1956; Sugarloaf Lake, Michigan). In each of these studies the estimate was constructed by an iterative procedure from successive measurements of standing crop. If, as is almost invariably true, there are long intervals between such measurements, the estimated rate of production coming from them is subject to large errors. This situation is improved to some extent if the data,

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[3] We are sympathetic with the preference of Thienemann (1954) and other European workers for the technically invalid name Chironomidae; not only is its alternative a phonic monstrosity, but also ". . . wir sind keine Philologen, sondern Biologen; und wenn die wissenschaftliche Verständigung durch das Prioritätsgesetz in manchen Dingen nicht nur nicht gefördert, sondern sogar gefährdet wird, so muss dieses 'Gesetz' eben dementsprechend umgestaltet werden!" (Thienemann 1954, p. 1).

instead of being used directly for the computation, can be fitted with a smooth function that one may reasonably extrapolate backward to the time of hatching and that will, with suitable manipulation, yield a single rate of production based upon all available information on the history of a given cohort. Such a method is proposed here, usable with any organism having a life-cycle with a pattern similar to that of the chironomids actually referred to.

Production of Organic Matter

One makes a useful approach to this problem by noticing that the product of the number of individuals in a cohort[4] and their mean weight at any particular time is a total weight equal to the standing crop at that time. Such a product may be represented as the area of a rectangle (Figure 1). A series of such rectangles, representing standing crops at various times, is generated by the curve obtained from plotting number of individuals against mean weight for the entire history of a cohort. It should be noticed here that number of individuals is necessarily monotonically decreasing with time and mean weight almost invariably monotonically increasing; cohort size will usually decrease monotonically with increasing mean weight.

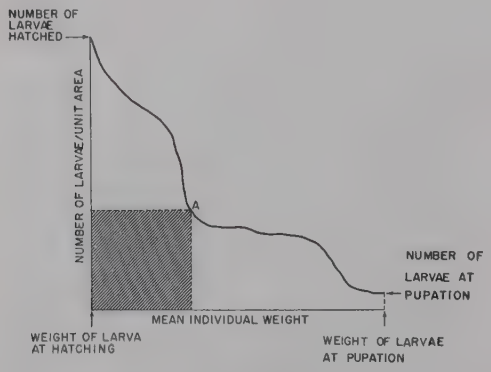

FIG. 1. Generalized relationship between mean larval weight and cohort size; standing crop (in units of weight) at the moment when the cohort passes through point A is equal to the area of the shaded rectangle.

Certain relationships and definitions follow from such a curve. Let M_t be the total number of individuals in a cohort that have died by time = t (measured in this instance from the day of hatching, on which we will call t =0), N_t be the number of survivors at t, Q_t be the mean weight of the survivors at t and let t_p be the point at which the insects pupate and leave the lake as adults, assumed to be the same for all members of the cohort.

Over any small increment of growth, ΔQ, at time t, the amount of material produced is $\Delta Q N_t$ (Figure 2; the increment in material is indicated by the crosshatched area), or, in the limit as $Q \rightarrow 0$, $N_t dQ$. The total quantity of material produced up to any time, t, during the lifetime of the cohort (exclusive of that used in respiration, which for the moment we will ignore) is obviously the sum of all such increments or the area under the weight-survivorship curve bounded on the right by the line $Q = Q_t$:

$$P_t = \int_{Q_o}^{Q_t} N_t dQ \qquad \ldots (1)$$

This quantity (P_t) is the same as an "actual net production" as the term is used by Clarke, Edmondson and Ricker (1946) and we shall continue to call it by that name.

We may now partition the various components of production in such a cohort, inventing some new terms for components having been designated previously by no particular names. We shall follow the usage of Clarke, Edmondson and Ricker in applying the qualifier "net" to quantities from which respiratory or catabolic losses have been deducted.

1. Area ACDE (Fig. 2): Actual net production (above).

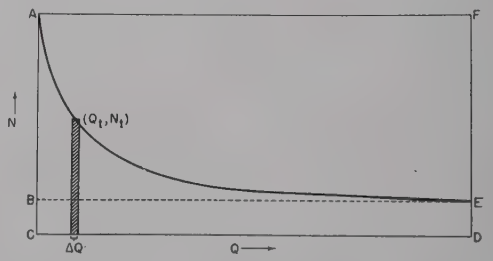

FIG. 2. Generalized relationship between mean larval weight and cohort size, defining quantities discussed in the text. An increment to actual net production during a growth increment, ΔQ, is equal to the area of the shaded rectangle.

2. Area BCDE: Pupal crop (an "actual net increase in standing crop" or "actual net increase" of Clarke, Edmondson and Ricker) $= Q_{t_p} N_{t_p}$.

3. Area ABE: Directly recycled production. This quantity represents material produced by the

[4] We use this term as it is commonly used, to mean a group of individuals all born or hatched at the same moment and living together, either in fact or hypothetically, under conditions identical in the time-specific sense, and ignore for the time being the question whether any such thing really exists in nature.

cohort, not realized in the pupal crop, but recycled to other organisms in the form of larvae eaten or decomposed during the life of the cohort.

4. Area ACDF: Potential net production. This represents the maximum quantity of material that could have been elaborated during the life of the cohort, and thus the total pupal crop, had there been no mortality ("potential net production" of Clarke, Edmondson and Ricker) $= N_o Q_{t_p}$.

5. Area AEF: Lost potential net production. This represents that portion of the potential net production never produced owing to deaths of potential producers

$$= \int_{Q_o}^{Q_{t_p}} M_t dQ$$

6. Area ABEF: Lost potential pupal crop. This final quantity represents the additional pupae that would have appeared had there been no deaths among the larvae $= M_{t_p} Q_{t_p}$.

The various expressions derived above may be related by summing and equating areas, for example, ACDE + AEF = ACDF, *i.e.* the actual net production plus the lost potential net production is equal to the potential net production of a cohort, or

$$\int_{Q_o}^{Q_{t_p}} N_t dQ + \int_{Q_o}^{Q_{t_p}} M_t dQ = N_o Q_{t_p}$$

and so on. Most of these relationships are now self-evident.

Theoretical Growth-Survivorship Curves

In practice, the form of the curve of mean weight plotted against cohort size is to be determined empirically. For the moment, however, we may use some conventional exponential equations describing growth and mortality to derive an analytical form for such a curve in an ideal population. To this end, let a growth-rate, k_g, be defined by:

$$k_g Q_t = dQ_t/dt \qquad \ldots (2)$$

where Q_t is the weight of an individual at time t, and let a mortality-rate, k_m, be defined by:

$$-k_m N_t = dN_t/dt \qquad \ldots (3)$$

where N_t is the size of the cohort at time t. Eliminating t from these two expressions, we obtain

$$k_g/dQ_t/1/\int/Q_t = -1/k_m \int dN_t/N_t + C$$

which is integrated to yield

$$Q_t^{-k_m} = CN_t^{k_g} \qquad \ldots (4).$$

If Q_o is the weight of the larva at hatching and N_o the initial size of the cohort, then:

$$C = \frac{Q_o^{-k_m}}{N_o^{k_g}}$$

whereupon (4) becomes, after both sides are raised to the power $-1/k_m$,

$$Q_t = \frac{Q_o}{N_o^{-k_g/k_m}} N_t^{-k_g/k_m} \qquad \ldots (5).$$

Curves obtained from solution of (5) for values of $k_g/k_m = 1, 2, 3, 4, 6$ and 8 are shown in Figure 3. The value $Q_o = 0.1$ mg and $N_o = 10^6$ were selected arbitrarily; neither of these quantities affects the general shape of the resulting curve.

It is evident from an inspection of Fig. 3 and equation (5) that:

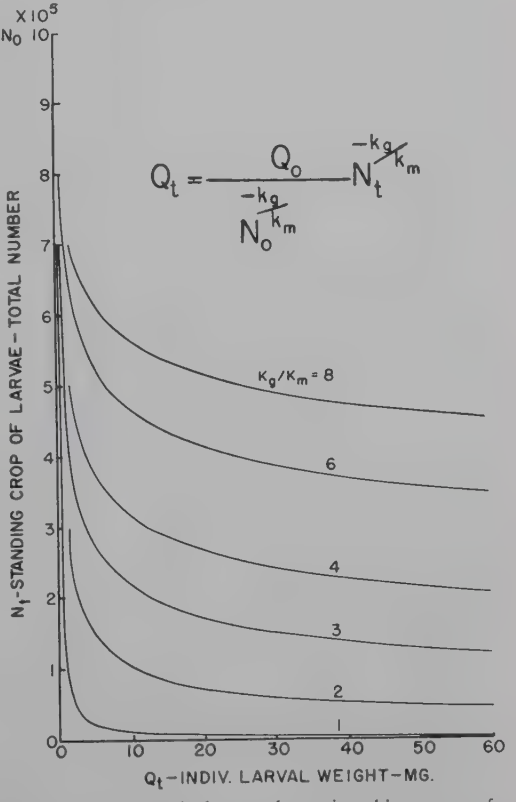

Fig. 3. Theoretical growth-survivorship curves for ideal cohorts derived from assumptions of exponential growth and mortality.

1. The shapes of these curves and thus of the characteristics of production within the cohort, depend entirely upon the ratio k_g/k_m; the absolute values of the two k's may vary widely, but so long as their ratio remains constant, the growth survivorship curve will trace out the same path.

2. With given N_o, Q_o and Q_{t_1}, the area under a curve (the actual net production) depends only upon the absolute value of the ratio k_g/k_m. The range $1 < k_g/k_m \leq 2$ is one in which very large relative changes in actual net production occur with very small changes in the value of the ratio.

Analysis of a Real Population

The data published by Anderson and Hooper (1956) for Sugarloaf Lake, Michigan, are useful for further analysis along the lines suggested above, particularly for the reason that these authors have computed a value for actual net production by an iterative method.

Tanytarsus jucundus (Walker), one of the littoral species studied by Anderson and Hooper, passes through but one generation per year in Sugarloaf Lake. Relevant data for the generation of 1953-1954 are given by them in their Table I. We have retained the units used there, expressing larval weights as ml of water displaced, and cohort sizes as numbers of larvae per 0.25 ft² (or numbers per standard 6-inch Ekman dredge-haul).

These data may be examined for conformity to the hypothesis that the ratio k_g/k_m is a constant; this is accomplished rather simply by rearranging (5) into the form

$$\log Q_t = \log Q_o + (k_g - k_m) \log (N_o/N_t) \quad . \quad . \quad . \quad (6)$$

which is linear in the logarithms of both variables. If k_g/k_m is constant, then all available points (Q_t, N_t) plotted in a double logarithmic grid ought to fall on a straight line. Such is true of the data of Anderson and Hooper (Figure 4) excepting the point for September. The fact that the data show no growth between August and September, a period that our own experience with *Chironomus plumosus* and *C. staegeri* in Lake Mendota leads us to believe may be one of rapid growth among midge larvae, suggests that perhaps the displacement of the September point is due to a defect in sampling or to an error of some other sort, although too close a comparison ought not to be drawn between the littoral *T. jucundus* and the abyssal *C. plumosus* and *C. staegeri*. The authors have not attached standard errors to their means and so little more than this can be said; the possibility is of course not excluded that some special set of circumstances did indeed halt growth entirely during this period and accelerate mortality. We shall assume for the purpose of continuation that the point is in error.

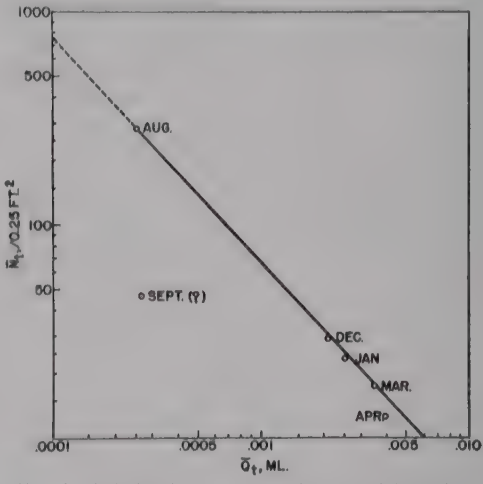

Fig. 4. Relation between mean larval weight and cohort size for *Tanytarsus jucundus* in Sugarloaf Lake, Michigan (data from Anderson and Hooper 1956), axes logarithmic.

The growth-survivorship curve for the generation of 1953-1954 (Figure 5) was constructed by taking appropriate points from Fig. 4; it is shown along with the data of Anderson and Hooper. Q_o was estimated to be approximately 0.0001 ml by applying a simple proportion to the data of their Table I and their Fig. 4.

The area under the curve of Fig. 5 is 0.247 ml/0.25 ft², determined planimetrically. This is the actual net production for the generation of 1953-1954. Anderson and Hooper estimate the same quantity as 0.1745 ml/0.25 ft² by computing first what we have called the directly recycled production, then adding this to the last measured standing crop of larvae, at the same time assuming this to be equal to the standing crop of pupae and to the crop of emerging adults. The d.r.p. had been computed by multiplying the difference between the numbers of larvae present in 2 successive samples by the average individual volume in the 2 samples, and summing such products over all pairs of successive samples.

We may now compute the other quantities defined above as follows:

1. Potential net production $= N_o (Q_{t_p} - Q_o) = 760(0.00385 - 0.0001) = 2.850$ ml/0.25 ft².

2. Pupal crop $= N t_1 (Q_{t_1} - Q_o) = 12 \times 0.00375 = 0.045$ ml/0.25 ft². (This is a "pupal" crop only if one makes the assumption that the crop of pupae is equal to the last measured crop

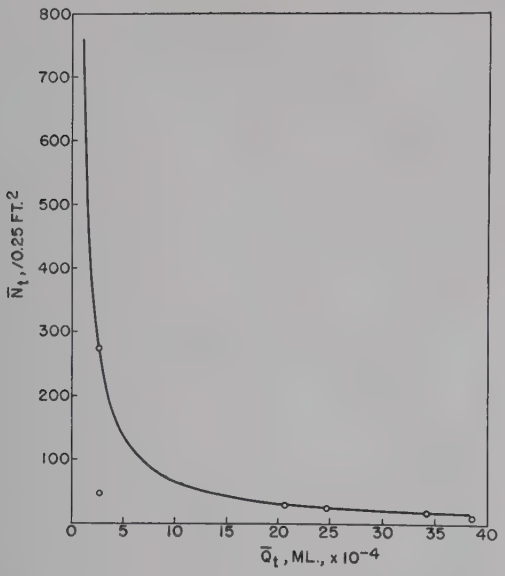

FIG. 5. Relation between mean larval weight and cohort size for *Tanytarsus juncundus* in Sugarloaf Lake, Michigan (data from Anderson and Hooper 1956), axes arithmetic.

of larvae. If one assumes no mortality during the pupal stage, this is also equal to the crop of emerging adults. Neither assumption needs to be challenged or defended here.)

3. Lost potential net production = —(a.n.p. — p.c.) = 0.247 — 0.045 = 0.202 ml/0.25 ft^2. (This last is equivalent to the "total mortality" of Anderson and Hooper, which they give as 0.1265 ml/0.25 ft^2.)

In addition to the foregoing quantities, certain ratios are of interest:

1. a.n.p./p.n.p. = 0.087, *i.e.* the cohort elaborated 8.7% of the organic matter that might have been produced had all larvae lived to the "pupal" stage (stage of the larvae at last measurement).

2. p.c./p.n.p. = 0.016, *i.e.* of the potential net production, only 1.6% was realized in the bodies of the "pupae" (final larvae).

3. d.r.p./a.n.p. = 0.818, *i.e.* of the actual net production, at least 81.8% remained to be recycled within the lacustrine biota, no more than 18.2% became available to an energy pyramid outside the lake.

A crude mortality rate for the cohort of larvae may be computed by obtaining N_o through extrapolation of the curve in Fig. 4, which proves to be about 760 larvae /0.25 ft^2 and comparing this with the known N_{tf} (12). The rate so obtained is 98.4% crude total mortality, a figure that seems quite credible.

DISCUSSION

The general applicability of the method outlined above depends of course upon the general tendency for a parameter corresponding to what we have called k_g/k_m to be constant. Where this can be shown to be true through demonstration of linearity in a double-logarithmic plot of the growth-survivorship curve, the whole problem of computing total production and its various fractions is considerably simplified. In fact, in such instances it is not necessary to use a planimeter; the actual net production is defined with equation (1) and N is given as a function of Q in equation (5), thus allowing a straightforward analytical solution of (1):

$$\text{a.n.p.} = P_t = \frac{N_o}{Q_o^{-k_m/k_g\left(1 - (k_m/k_g)\right)}} \times \left[Q_{tf}^{1 - (k_m/k_g)} - Q_o^{1 - (k_m/k_g)} \right] \quad \ldots (7)$$

from which the a.n.p. may be calculated directly, the data providing the means for giving numerical values to all the constants in this expression. Where the double-logarithmic plot is not a straight line, the use of a planimeter on a curve hand-fitted to an arithmetic plot of mean weights against numbers ought still to effect some considerable simplification in the computation of actual net production. The general method is of little value in dealing with populations having very complex age-structures, in which groups corresponding reasonably closely to real cohorts cannot conveniently be separated and handled individually.

It would be of some interest to discover how many natural populations show a constant k_g/k_m. For the data of Anderson and Hooper, the value of this ratio is 0.933, and it appears to be relatively constant over the life of the cohort. The only other estimate known to us is that of Dugdale (1955) for *Chironomus plumosus* in Lake Mendota; he obtained by a method different from ours a value of 0.002 for k_g and of 0.001 for k_m, thus of about 2. for the ratio k_g/k_m. A considerable difference in what might be thought of as a special kind of "efficiency of production" is implied by the difference between the two values, *C. plumosus* in Lake Mendota elaborating a larger actual net production per unit of hatched weight than *T. juncundus* in Sugarloaf Lake. This conclusion ignores the possibly compensating differences in, for example, respiratory efficiency between the two populations.

Summary

A model is described for use in computing the various fractions of production for populations of organisms in which the life-history is similar to that of the various species of Chironomidae at least in the sense that a population consists of a single cohort or of a small number of easily distinguishable cohorts. The model is based upon the relationship between mean larval weight and size of the larval population throughout the aquatic phase of the life-history, treating time and age as implicit variables only. The fractions of total production for such a population, such as emergent crop, directly recycled production, and actual net production are defined, and the model is used to obtain expressions for computing their values. A possible deterministic form for the function relating mean weight and cohort size is derived from some simple assumptions of exponential growth and mortality:

$$Q_t = \frac{Q_o N_t^{\,-\,k_g/k_m}}{N_o^{\,-\,k_g/k_m}}$$

where Q_t is mean larval weight and N_t is cohort size and other quantities are constants. This form is compared with the form observed in data from an independent study of a population of *Tanytarsus jucundus* (Anderson and Hooper 1956) and found to be in good agreement.

References

Anderson, R. O. and **F. F. Hooper.** 1956. Seasonal abundance and production of littoral bottom fauna in a southern Michigan lake. Trans. Amer. Microsc. Soc. **75**: 259-270.

Borutzky, E. V. 1939. Dynamics of the biomass of *Chironomus plumosus* in the profundal of Lake Beloje. Hydrometeorol. Serv. U.S.S.R. Proc. Kossino Limnol. Sta. **22**: 156-195.

Clarke, G. L., W. T. Edmondson and **W. E. Ricker.** 1946. Mathematical formulation of biological productivity. Ecol. Monogr. **16**: 336-337.

Dugdale, R. C. 1955. Studies in the ecology of the benthic Diptera of Lake Mendota. Ph.D. thesis. University of Wisconsin.

Lundbeck, J. 1926. Die Bodentierwelt Norddeutscher Seen. Arch. f. Hydrobiol. Suppl. to Vol. 8. pp. 1-470.

Thienemann, A. 1954. Chironomus. Die Binnengewässer. Vol. 20.

DELAYED HATCHING IN STRANDED EGGS OF MARSH KILLIFISH, *FUNDULUS CONFLUENTUS*[1]

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The presence of small fish among mosquito larvae hatched by flooding dry sods cut from salt marshes long exposed by the recession and evaporation of flood waters had been observed several times by both J. S. Haeger and W. L. Bidlingmayer of this laboratory. A recurrence of the phenomenon led the writer, with the help of J. S. Haeger, to investigate it systematically in order to determine whether the fish were introduced with the water used to flood the sod samples, were somehow resident in the sods as hatchlings, or whether larval fish as well as mosquitoes first hatched upon being flooded in the laboratory.

It will be shown that the exposed, stranded eggs remain viable for months, and hatch following flooding, without which hatching is postponed indefinitely. This provides an ecological context for experiments on hatching physiology, and invites comparison with somewhat analogous conditions among certain South American and African fishes of the same family (Cyprinodontidae) and the tide-controlled spawning of the grunion, an atherine fish of California.

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Procedures and Results

Additional sods were cut near the one obtained for hatching mosquito larvae which upon immersion in water had unexpectedly yielded fish larvae as well. Other sods were cut elsewhere in the general habitat, a *Borrichia* swale from which autumn flood waters (rain) had receded at least a month and one-half before, and probably earlier. Sods cut from the dried-up swale on December 9, 10, 15 and 18, yielded a total of 65 fish larvae

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after being flooded with tap water. The last vestige of standing water had disappeared from the swale shortly after mid-October at the latest, and it was known to have remained exposed thoughout November and December.

By clipping off emergent vegetation, raking up bottom litter, and separately flooding both sod proper and litter and cut vegetation, it was established that all were productive of larval fish. From relatively few observations, sod proper and litter were found more productive than cut vegetation. Moist, matted algae proved more so than the rest of the bottom litter which consisted chiefly of stems and other plant fragments. Thereafter, algal patches alone were gathered and flooded. These were gray, pale or bright green according to amount of moisture. Gray patches alone invariably failed to yield larval fish, but relatively few of these were flooded.

Fish larvae were seen 15 minutes after flooding but mostly within 30 minutes. Those first sighted within 30 minutes may have been free-swimming in 15 minutes as the others were, since they are inconspicuous unless they swim up to the edges of the flooding pan, and some at least remain motionless at first. A long search among algal patches which had yielded fish upon flooding finally disclosed an evacuated fish-egg chorion attached to the algal filaments. This encouraged a painstaking examination with stereoscopic microscope of unflooded algal patches from likely oviposition sites, which was at length rewarded by the discovery of an unhatched egg. The chorion was 1.6 mm in diameter and not obviously thicker or tougher than that of *Fundulus heteroclitus*. It was caught in the interstices of the filaments on the underside of the algal patch (Figure 1). After immersion in water, this egg hatched. The freed larval fish was of the same size and developmental stage as those obtained from the other sods or their components. It remained stationary at first, respiring vigorously and vibrating its pectoral fins. A stream of minute particles and microorganisms, on which it seemed to be feeding, was thus drawn in through its mouth. Another larval fish the day it hatched ingested a first instar mosquito larva, *Aedes aegypti*. None of the larval fish closely examined had noticeably unabsorbed yolk sacs, and thus had seemingly consumed much of their food reserves before hatching. Most of the fish larvae obtained from sod flooding were reared to sexual maturity; others were preserved for studies of growth and differentiation. Fourteen were lost, 7 during transfer to another aquarium and 7 unaccountably. All of the remaining 51 proved to be marsh killifish, *Fundulus confluentus* Goode and Bean.

FIG. 1. An egg of the marsh killifish, *Fundulus confluentus*, attached to the filaments on the underside of a patch of algae stranded on the ground since the flood waters disappeared a month and one-half or more before.

Sampling Sites

In all 14 productive sods or sod components were processed. These were obtained from 3 sampling sites equally spaced along a north-south line about 200 feet long. All were close to the highest elevation within the formerly flooded swale, at or near its margin. The southernmost site, at the berm of a pothole, yielded 17 fish larvae, 12 from an intact sod, 4 and 1, respectively, from matted algae alone. The northernmost site, at the base of a clump of sedge, *Fimbristylis castanea* (Michx.), near the edge of the swale, yielded 6. The middle site (Figures 2 and 3) yielded 42 larvae from 8 samples taken within an over-all area of 75 square feet. Thirty-nine of these were from 6 samples (sods or algal patches) within 20 square feet, and 31, from 5 samples within 10 square feet, evidently the focus of egg deposition at this location. Some of the 42 larvae were from samples contiguous with saw-palmettos, *Seranoa repens* (Bart.), and their prostrate trunks bordering the swale; none came from samples over 8 feet from this border. In the over-all area of the swale an unrecorded number of sods failed to produce larval fish when flooded, but additional observations, when conditions permit, will be needed for a definitive description of the preferred deposition sites.

Description of the General Habitat

The large central basin of the swale (Figure 3) was uniformly covered by an evenly mixed stand of sea-ox-eye, *Borrichia frutescens* (L.), and water-hyssop, *Bacopa Monnieri* (L.). Surrounding it at the next higher elevations was a broad expanse of the same 2 plants interspersed with evenly but widely spaced tufts of saw-grass,

FIG. 2. A close-up of the bottom of the swale at the middle and most productive sampling site. Sod sampling has left bare spots. Compare with the text and figure 3.

FIG. 3. The view northward from the middle sampling site and across the basin of the swale to its edge. The net with clamp-board marks the center of the middle sampling site. Compare with the text and figure 2.

Cladium jamaicense Crantz, and sedge, *Fimbristylis castanea* (Michx.). The highest elevation formerly flooded is typified by our middle and most productive sampling site (Figures 2 and 3). Over most of it, the sedge, sea-ox-eye, and sawgrass were about equally present, with the first slightly more, and the last, slightly less abundant than sea-ox-eye, and with traces of a carpet of new water-hyssop seedlings. The westernmost sods from this site were adjacent not only to sawpalmettos, but also to sea-myrtle, *Baccharis halimifolia* L., wax myrtle, *Myrica cerifera* L., and Brazilian peppertree, *Schinus terebinthifolius* Raddi.

The lowest elevation of the swale is 0.78 feet (24 cm), and the highest (at the sampling site just referred to), 1.45 feet (44 cm) above mean sea level. The average level of Indian River is somewhat above mean sea level and the mean daily tide range at this point is somewhat less than one foot. Northeast and southeast of the swale there are ill-defined barriers over which, during prolonged intervals of heavy rainfall, connections may form between fresh pluvial water spilling out of the swale and brackish tidal water flowing in from Indian River. Physiographic and botanic features both indicate that the flow is usually from the swale across the low hammock bordering it and into the *Batis-Salicornia* salt marsh adjacent to the saline waters of Indian River to the east, and of a canal to the south. The reverse flow is to be expected only occasionally, during years when unusually high storm winds reinforce high tides. Most of each year the barriers prevent flow in either direction, but, usually in early autumn, when water levels rise even slightly above these barriers, pluvial and tidal waters meet, and brackish-water fishes emigrating from Indian River shallows and tide-water ditches may repopulate the swale. In January following the termination of our sod sampling, the swale was refilled by heavy rainfall (see below). Its salinity was then 2.5 ‰ (1.0011 specific gravity at 15° C) and, after the swale had dried down to a few puddles in February, it had increased to only 7.6 ‰ (1.0050 specific gravity).

The Longest Record of Delayed Hatching

An additional notable single larva of the same species was obtained from a sod cut on September 19, in another area and habitat 5 miles away. This sod was kept on a flat board out-of-doors but shaded and protected from rainfall under a wide roof and was lightly sprinkled with tap water about once a week. It was flooded on December 23, and yielded a larval fish. It had not been anticipated that fish would be found in the flooding pan, which was used to procure a hatch of mosquitoes, *Aedes taeniorhynchus* and *A. sollicitans*, and the fish was overlooked until December 30. When examined the 30th, it was in a stage of development comparable to the week-old larvae preserved from the swale sod samples, and was no doubt hatched on December 23. This represents an incubation period, including an interval of delayed hatching, of 95 days (3 months and 5 days) exclusive of the unknown interval following deposition during which the eggs were under water. It is pertinent to mention here that the interval between deposition and hatching for the other larvae considered above undoubtedly exceeded a month and one-half, which is a conservative estimate of the time elapsing after the swale had become completely exposed. A part of the incubation period was perforce within the interval before the water receded from the deposition sites, which were in all cases at the marginal and highest elevations of the swale, and would thus have

been exposed long before the swale as a whole dried up.

The Osmoregulatory Status of Fundulus confluentus

Since *Fundulus confluentus* has been categorized (Briggs 1958) as a freshwater fish, and is described here entering a rain-filled swale and depositing its eggs there, it is necessary to assert that, on the contrary, the species is euryhaline, with a preference for brackish water. In Indian River and St. Lucie counties, Florida, it is taken most commonly on salt marshes and in their ditches, which communicate freely with the open saline waters of Indian River. On the barrier islands to the east, where the species abounds, there is no appreciable watershed, and salinities approach that of fresh water only locally and temporarily after torrential autumn rainfall. Otherwise, salinities in salt-marsh ponds and shallow ditches equal or exceed those of Indian River, owing to evaporation during hot periods with low rainfall. On the Gulf coast, Kilby (1955) obtained over 80% of his Cedar Key specimens at 20-30 ‰ and over 50% of his Bayport specimens at 10-30 ‰ but he mentions others obtained from inland fresh waters many miles from the coast in Levy County. Miller (1955) refers to the species as typically in brackish, but entering fresh and salt water, and Brown (1956), as typically in brackish; both give its distributions as Chesapeake Bay, Maryland, southward to Key West and northward to a few miles west of Pensacola Bay. Bailey, Winn, and Smith (1954) took it in the Escambia River, Florida, where surface and bottom salinities were 4.5 and 24.4 ‰, respectively. They place it in the category of marine or brackish-water fishes sporadically invading strictly fresh water, most likely for brief periods and short distances usually, and seldom exceeding tidal water. It has not been taken by the writer in savannahs of Indian River and St. Lucie counties nor in freshwater ditches in Fellsmere, both of which contain the freshwater species *F. chrysotus* and *F. notti lineolatus,* and neither of which is far from the coast. It is evident from the present report that *Fundulus confluentus* is capable of reproduction in fresh water, and individuals have been kept in fresh water indefinitely by the writer, so that its preference for brackish water may be conditioned by limiting factors other than osmoregulatory stress.

Although no field observations of breeding are recorded for this species, it probably deposits eggs in brackish water as well as in accumulations of fresh water from surface run-off as described here. Males in breeding color occur in our collections of March, April, June, July, and September. From his data on the growth of *Fundulus confluentus,* Kilby (1955) inferred a long breeding season, high mortality, and a life span of one season for the majority of individuals. The writer has experimental evidence indicating that reproductive activity begins as early as February, but is suspended at least during the preceding 2 months. On the barrier islands between Indian River and the ocean, *F. confluentus* is most abundant toward the side of the ditch system away from the Indian River shore line, but such ditches are commonly just behind the ocean beach barrier, *e.g.* on Hutchinson Island (Harrington and Bidlingmayer 1958), where the watershed is virtually nil and freshwater run-off or seepage would be negligible. The only significant dilution would result from prolonged heavy rainfall, usually an autumnal phenomenon, which would at best be effective in these ditches merely within the latter part of the presumably long spawning season.

The Climatological Background of Egg-deposition and Hatching

Figure 4 summarizes climatological data for 6 months, recorded within a quarter of a mile of the oviposition sites described, at the Entomological Research Center of the Florida State Board of Health, in Vero Beach. Dates on which sods with stranded eggs were cut are designated at the top of the figure. It will be recalled that the sod cut on September 19 was not flooded until December 23, whereas the other sods, cut on 4 dates between December 9 and 18, were flooded the day cut. Tidal waters did not reach the swale during the 6 months concerned, but the swale doubtless overflowed into the tidal marshes to the east during the protracted heavy rainfall of August-September. The January rains, which refilled the swale, were insufficient for overflow into the tidal waters, and the flooded area within the swale had contracted to one-fifth of its maximum extent by February 10, and to a small pothole by the 20th.

The September 19 specimen, flooded and hatched December 23, clearly demonstrates that eggs spawned during the August-September rainy period were capable of surviving out of water long enough to be hatched by the January rains, the peak of which fell only 11 days after this particular egg was hatched in the laboratory. Nor is there any reason to doubt that those eggs hatched in the laboratory December 9-18 would have hatched if left in the swale, especially since recently hatched larval *F. confluentus* were collected in the reflooded swale after the January rainfall. When

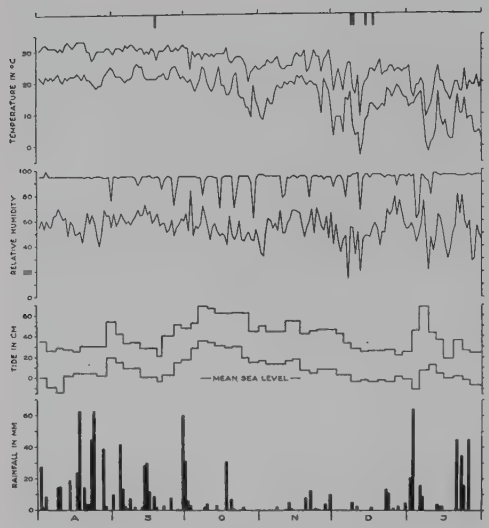

FIG. 4. Local climatological data for six months of 1957-1958: daily maximum and minimum temperatures and relative humidities, semi-weekly maximum and minimum tide levels, and daily rainfall records. Heavy vertical lines at the top of the figure mark the dates on which sod samples were cut. Those cut in December were flooded in the laboratory the day cut, that cut in September was flooded on December 23. Compare with the text.

first discovered, January 29, these ranged in size from slightly larger than 2-week-old, to slightly larger than 4-week-old specimens preserved from those reared from the egg in the laboratory.

The daily maximum and minimum temperatures and relative humidities plotted in Figure 4 were recorded in an instrument house 2 meters off the ground and one-quarter of a mile from the swale. Another hygrothermograph was set up unhoused on a hummock projecting into the swale. The relative humidities recorded at the swale deviated no more from those plotted here than could be attributed to instrument inaccuracy, but the temperatures recorded at the swale were not infrequently 3-5° more extreme. These differences are partly ascribable to the fact that the swale hygrothermograph was unenclosed. Relative humidities in the microclimate were no doubt higher than those of the macroclimate, and the extremes of temperature somewhat greater, but no data are available on the microclimate. Since the stranded eggs survived this unsually cold Florida winter, they would be able to survive any normal winter here. At Fort Pierce, 10 miles away, during a 15-year period, the average number of days per winter (October through April) on which temperatures fell below 4.4° C was five, whereas during 1957-58 they fell below this temperature 5 days in December alone, 4 in January, and 10 in February.

Ecological and Physiological Significance

This appears to be the first record of a Nearctic cyprinodont with prolonged delay in hatching under natural conditions. Even among fishes with protracted egg dormancy, the marsh killifish, *Fundulus confluentus,* is unique in that its eggs are not buried in mud or sand but left exposed to the atmosphere, stranded on the ground among plant litter when the water recedes. The eggs of salt-marsh mosquitoes (*Aedes* spp.) lying alongside them, also ready to hatch on being flooded, differ in having been deposited on the ground between floodings rather than in water. Amphibian eggs, *e.g.* those of the salamander, *Ambystoma opacum,* have wintered over in a viable state exposed to the atmosphere (Noble and Brady 1933), but this is of infrequent occurrence (Bishop 1941). Salamander eggs have hatched after 151 days out of water in the laboratory; others out of water over a year contained live larvae (Noble and Brady 1930, 1933).

The specialized annual cyprinodonts of South America, *Cynolebias* spp., deposit their eggs in the bottoms of isolated mud holes and the like where, in the dry season, they come to lie under a top crust, tiding over the species locally (Myers 1942). In the wet season these hatch in the softened mud, and the fry grow to maturity and spawn before this adult population is destroyed during the dry season following, when standing water disappears. The life cycles of African cyprinodonts, *Aphyosemion caeruleum* and *Nothobranchius* spp., evidently entail much the same adaptation, including tough-shelled eggs (Myers 1942). Hatching of the Indian cyprinodont, *Oryzias melastigma,* can be delayed although the eggs remain in water (Jones 1944). The usual incubation period is 8-14 days, yet, if the water is not changed during the hot season, hatching may be delayed up to 6 weeks; when water of lower salinity is added to the experimental aquarium, normal fish hatch at once. Jones conjectured a bursting of egg membrances with sudden change in osmotic pressure, but compare *Oryzias latipes* below. The early-hatched larvae differ from the late-hatched, in having a little yolk, less pigmentation, and fewer fin-rays.

Among fishes with deferred hatching, the best known ecologically (Thompson and Thompson 1919, Clark 1925) is an atherine fish of the California coast, the grunion, *Leuresthes tenuis.* Mid-

August to mid-January it has only immature eggs. From an intermediate class of eggs first developing January-February and maintained throughout the spawning season, March to August, a maturing class is withdrawn and spawned out every 15 days. This interval is such that spawning begins just after turn of tide during the lower (bright moon) series of high tides but somewhat later than turn of tide during the higher (dark moon) series of high tides. Thus the eggs are always deposited near the same point on the beach profile so that after 2 weeks the lower series of high tides washes out the eggs deposited during the higher series, and *vice versa*. During the interim of low tides, the eggs are above tide level in moist sand 4 inches beneath the surface.

When enclosed in a moist atmosphere, grunion eggs on the surface of sand are as proof against desiccation as those buried. Eggs freshly dug up near normal hatching time hatch in 4-5 minutes, but must first be freed from the sand. Eggs kept in sand one month and 5 days hatched when freed from sand in water, 2 weeks after normal hatching time, but hatching was slower and viability less (Thompson and Thompson 1919). When kept in standing or running sea water or in sand, they have an incubation period of 7.5 days, a week shorter than in nature, but most of those in sand or in quiet water do not hatch unless subjected to a stream of running water (David 1939). A fuller understanding of the hatching mechanism awaits technically refined experiments.

Onset of hatching in fishes is accompanied by a complex of obscurely interrelated phenomena (Smith 1957), but has a common though not universal referent in transitory hatching glands that secrete a proteolytic enzyme eroding the egg chorion. Such glands, found also in amphibians (Noble and Brady 1930) are widespread among fishes, *e.g.*, in the families Acipenseridae, Salmonidae, Cyprinidae, Gasterosteidae, Syngnathidae, Cyprinodontidae, Symbranchidae, Percidae, Anabantidae, Gobiidae, Gobiesocidae (Moriwaki 1910, Wintrebert 1912, Gray 1926, Bourdin 1926, Armstrong 1936, Hayes 1942, Ishida 1944, Wu and Liu 1945; Smith 1947, Wu and Wang 1948, Zotin 1954). They are apparently lacking in the mouth-breeding cichlid, *Tilapia macrocephala* (Shaw and Aronson 1954), and in the cyprinid, *Rhodeus ocellatus,* which hatches at a developmental stage far earlier than that in which such glands commonly differentiate (Chang 1948).

Armstrong (1936) prevented the hatching of *Fundulus heteroclitus* by inducing a non-patent mouth, thus excluding the hatching enzyme which is elaborated by bucco-pharyngeal glands from the perivitelline space, or by eliminating bodily movement with KCl or chloretone. He concluded that hatching requires both a weakening of the chorion by the enzyme and its rupture by bodily movement. Milkman (1954) delayed hatching indefinitely by keeping eggs at a high oxygen tension in sea water. When transferred to normal sea water, they hatched in 7½ minutes. The fate of *F. heteroclitus* eggs in nature is little known, and it remains to be found out whether they are ever exposed to natural conditions of semi-desiccation.

Ishida (1944a and b), experimenting on another cyprinodont, *Oryzias latipes,* demonstrated what others had inferred, that the hatching glands produce the enzyme and that they disintegrate shortly before hatching. He found that the disintegration (secretion) of these holocrine glands results from the mechanical action of the water flow produced by onset of opercular movement, which he simulated with a stream of water through a glass capillary. Both opercular movement and hatching were inhibited by chloretone, although hatching occurred when bodily but not opercular movement was repressed with a barbiturate, indicating that opercular movement is the more important factor. Glands isolated in nearly isotonic solution (M/8 NaCl) remained unchanged, but broke down in hypotonic solutions (M/28 to M/128), the more hypotonic, the sooner. In isotonic saline, the glands broke down in intact eggs if opercular movement began, so that osmotic pressure of the surrounding medium is not the chief cause of their disintegration. Opercular movement and hatching were inhibited by M/4 KCl. In eggs about ready to hatch, they are accelerated by M/8 KCl (nearly isotonic), evidently through stimulation of opercular movement, but immersion for several days in the same concentration prior to normal hatching time inhibited hatching. This was attributed by Ishida to a narcotizing or paralyzing effect caused by the diffusion of KCl into the muscles. Hatching was accelerated by M/4 NaCl, which seemed to accelerate opercular movement, whereas isolated glands break down only at concentrations more hypotonic than M/16 NaCl. Opercular movement and hatching were inhibited by M/3 to M/6 $CaCl_2$, but M/8 $CaCl_2$ had no more effect than tap water. Onset of opercular movement was accelerated by 0.001 N KCN and hatching occurred; it was also accelerated by 0.01N KCN, but hatching did not follow since the enzyme is inhibited by this concentration of KCN.

Mature embryos with hatching deferred and viability sustained far beyond the minimal incubation period are aptly termed latent embryos, a

recent usage with reference to mosquito eggs (Horsfall, Lum, and Henderson 1958) to avoid implications of diapause, a different phenomenon. A potentiality for such latency would seem to be widespread among cyprinodonts, which in this respect are approached only by the grunion so far as is presently known. As the literature just considered indicates, if latency is ended by onset of opercular movement, the latter could be conditioned in different ecological situations by a change in one of several variables, such as pO_2 and probably pCO_2 or concentrations of electrolytes with certain cations. In the case of *Fundulus confluentus,* stimulation and inhibition of hatching might be governed by different environmental factors according to whether the eggs are in or out of water. In this context, experiments have been planned to supplement the present observations.

The oviposition sites of *Fundulus confluentus* described here were such that most if not all of the hatchlings would have perished within a few weeks, but the additional record from another area shows that deferred hatching in such stranded eggs is not an isolated phenomenon, and it is unlikely that so pronounced a capacity for prolonged latency is accidental. Since these observations were made, a *Fundulus grandis* hatchling was obtained by flooding litter from an exposed Indian River beach horizon reached only by high (spring) tides. As the northern *Fundulus heteroclitus* and the southern *Fundulus grandis,* which are sympatric only in the Matanzas Inlet in northeastern Florida, are closely related, it is possible that hatching may likewise be deferred in stranded eggs of *F. heteroclitus.*

Summary

Viable eggs of marsh killifish, *Fundulus confluentus,* which hatched within 15-30 minutes after immersion in water, were obtained in sods out of water 2 to 3 months. The oviposition habitat was a formerly rain-filled swale with transitory connections in autumn with tidal water, giving temporary access to brackish-water fishes. Deposition sites were at the forefront of the prior flooding, at the highest elevations, and thus the first to be exposed when the swale dried down. Stranded eggs survived the severest Florida winter in many years, some hatching after the swale was reflooded by January rains. Although it had spawned here in fresh water from rainfall run-off, *F. confluentus* is euryhaline with a preference for brackish water, and during its evidently long spawning season, doubtless oviposits also in brackish waters, where it abounds in regions without access to fresh water. Except for the celebrated grunion (Atherinidae), delayed hatching of fishes in nature is identified with the family Cyprinodontidae, but reported heretofore only of African, South American, and Indian forms. Deferred hatching of *F. confluentus* differs from that of the other cyprinodonts and of the grunion in that its eggs await hatching not in sand, mud, or water but on the ground surface exposed to the atmosphere as do those of salt-marsh mosquitoes. Experimenters have both stimulated and inhibited hatching of fishes by manipulating such factors as oxygen tension and the concentrations of specific electrolytes, but experiments on the physiology of hatching have not been accompanied by studies of its ecology. The incidence of *F. confluentus* eggs both in and out of water and the extremely prolonged latency of the embryos uniquely suit this species for studies of the physiological ecology of hatching, which should provide fruitful analogies for the student of salt-marsh mosquito hatching.

References

Armstrong, P. B. 1936. Mechanism of hatching in *Fundulus heteroclitus.* Biol. Bull., **71:** 407.

Bailey, R. M., H. E. Winn, and C. L. Smith. 1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proc. Acad. Nat. Sci. Philad., **105:** 109-164.

Bishop, S. C. 1941. The salamanders of New York. New York State Mus. Bull. **324:** 1-365.

Bourdin, J. 1926. Le Mécanisme de l'éclosion chez les Téléostéens. IV. Physiologie du liquide périvitellin des oeufs de Téléostéens à l'éclosion. Compt. Rend. Soc. Biol. Paris. **95:** 1242-1243.

Briggs, J. C. 1958. A list of Florida fishes and their distribution. Bull. Fla. State Mus., **2:** 222-318.

Brown, J. L. 1956. A key to the species and subspecies of the cyprinodont genus *Fundulus* in the United States and Canada east of the continental divide. J. Wash. Acad. Sci., **47:** 69-77.

Chang, H-W. 1949. Life history of the common Chinese bitterling, *Rhodeus ocellatus.* Sinensia, **19** (1-6) : 12-22, 1948.

Clark, F. N. 1925. The life history of *Leuresthes tenuis,* an atherine fish with tide controlled spawning habits. Calif. Div. Fish and Game, Fish. Bull. **10:** 1-51.

David, L. R. 1939. Embryonic and early larval stages of the grunion, *Leuresthes tenuis,* and of the sculpin, *Scorpaena guttata.* Copeia **(2):** 75-81.

Gray, J. 1926. The growth of fish (1). The relationship between embryo and yolk in *Salmo fario.* J. Exptl. Biol., **4:** 215-225.

Harrington, R. W., Jr. and W. L. Bidlingmayer. 1958. Effects of dieldrin on fishes and invertebrates of a salt marsh. J. Wildlife Management, **22:** 76-82.

Hayes, F. R. 1942. The hatching enzyme of salmon eggs. J. Exptl. Zool., **98:** 357-373.

Horsfall, W. R., P. T. M. Lum, and L. M. Henderson. 1958. Eggs of floodwater mosquitoes (Diptera: Culi-

cidae) V. Effect of oxygen on hatching of intact eggs. Ann. Entomol. Soc. Amer., **51**: 209-213.

Ishida, J. 1944a. Hatching enzyme in the fresh-water fish, *Oryzias latipes*. Annot. Zool. Japon., **22**: 137-154.

— . 1944b. Further studies of the hatching enzyme of the fresh-water fish, *Oryzias latipes*. Annot. Zool. Japon., **22**: 155-164.

Jones, S. 1944. On the occurrence of diapause in the eggs of Indian cyprinodonts. Current Science, Bangalore, **13**: 107-108.

Kilby, J. D. 1955. Fishes of two Gulf coastal marsh areas of Florida. Tulane Stud. Zool., **2**: 175-247.

Miller, R. R. 1955. An annotated list of the American cyprinodontid fishes of the genus *Fundulus*, with a description of *Fundulus persimilis* from Yucatan. Occ. Pap. Mus. Zool., Univ. Mich., **568**: 1-25.

Milkman, R. 1954. Controlled observations of hatching in *Fundulus*. Biol. Bull., **107**: 300.

Moriwaki, I. 1910. Dai 3 Kwai Hokkaido Suisanshikenzyo Zigyohokoku: 524. [In Japanese; quoted by Ishida, 1944a.]

Myers, G. S. 1942. Studies of South American freshwater fishes. I. Stanford Ichthyol. Bull., **2**: 89-114.

Noble, G. K. and M. K. Brady. 1930. The mechanism of hatching in the marbled salamander. Anat. Rec., **45**: 274.

—. 1933. Observations on the life history of the marbled salamander, *Ambystoma opacum* Gravenhorst. Zoologica (New York), **11**: 89-132.

Shaw, E. S. and L. R. Aronson. 1954. Oral incubation in *Tilapia macrocephala*. Bull. Amer. Mus. Nat. Hist., **103**: 379-415.

Smith, S. 1947. Studies in the development of the rainbow trout (*Salmo irideus*). I. The heat production and nitrogenous excretion. J. Exptl. Biol., **23**: 357-373.

— . 1957. Early development and hatching. *In* The physiology of fishes. Vol. **2**: 323-359. New York, Academic Press.

Thompson, W. F. and J. B. Thompson. 1919. The spawning of the grunion (*Leuresthes tenuis*). Calif. Div. Fish and Game, Fish Bull., **3**: 3-29.

Wintrebert, P. 1912. Le mécanisme de l'éclosion chez la truite arc-en-ciel. Compt. Rend. Soc. Biol. Paris, **72**: 724.

Wu, H. W. and C. K. Liu. 1945. Integumentary serous glands and eclosion of larval *Monopterus*. Science Record, **1**: 611-616.

Wu, H. W. and T. H. Wang. 1949. On the ocurrence and significance of the anti-proteolytic substance in the embryos of fishes and frogs near hatching. Sinensia, **19** (1-6): 6-11, 1948.

Zotin, A. I. 1954. Mechanism of production of perivitelline fluid by eggs of salmonid fishes. Doklady Acad. Nauk, S. S. S. R., **96**: 421-424.

SOME ECOLOGICAL CHARACTERISTICS OF ANTS IN NEW GUINEA RAIN FORESTS[1, 2]

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INTRODUCTION

The purpose of the present paper is to describe in a preliminary way the ecology and local distribution of the ant fauna of the Papuan rain forests and in so doing to introduce several classificatory systems that can be employed in future descriptive ecological work. The account is entirely descriptive and comparative in nature. The author has not attempted to accomplish an intensive analysis of any aspect of the "community organization," and indeed it is probably true that no such analysis could be undertaken without thorough autecological studies of many individual species over a period of years. Nevertheless, there are several good reasons for presenting the available material in a compendious form, however fragmentary may be the accounts of individual species. First should be mentioned the extremely poor condition of our present knowledge of the biology of most of the genera and species that make up the huge Papuan faun. Beyond the early account of the ecology of New Britain ants by Dahl (1901), there exist only a few scattered, incomplete references to individual species, and these are usually appended to taxonomic studies. In any broad consideration of the evolution of adaptation and behavior of the world ant fauna, this scarcity of information on the Papuan fauna has always formed a major gap. Further, ants are an influential part of the biotic environment of most animal species in New Guinea, as they are in most tropical rain forest areas. Knowledge of the biology of at least the dominant ant species should form an important part of the background of future rain forest ecological studies, including further autecological studies of ant species. Finally, and perhaps most importantly, summaries of community ecology of the type proposed here will serve the purpose of contributing to comparative studies of faunal structure in different zoogeographic regions. Information relating to relative abundance and the

[1] Field research was supported in part by a grant from the Museum of Comparative Zoology, Harvard University.

[2] Grateful acknowledgment is made to Dr. William L. Brown and Dr. Mary Talbot for critically reading the manuscript and offering many helpful suggestions.

extent and nature of local adaptive radiation is essential to the future ecological refinement of zoogeographic studies.

The taxonomic basis of part of the present work, along with a gazetteer of collection localities, has been given in a series of earlier publications (Wilson 1957a, 1957b, 1958a, 1959; Wilson and Brown 1956, Brown and Wilson 1957, Brown 1958). The ecological studies reported in the present paper were centered in a tract of primary lowland rain forest located between the Busu and Bupu Rivers, east of Lae, Mandated Territory of New Guinea. At the time of the author's visit, during April and May, 1955, this area was especially favorable for the study of the endemic ant fauna. In the previous year the first bridge strong enough to support motor vehicles had been built across the Busu River, and the road from Lae extended into the rain forest beyond. The South Pacific Lumber Company was in the process of cutting tractor trails in all directions through the forest and had made considerable headway in high-grading the largest trees. Both virgin forest tracts and new clearings were accessible for ground collecting, while the trunks and tops of freshly felled trees could be examined in quantity for arboreal ants.

The ant fauna of the Busu-Bupu area is perhaps the richest ever recorded for a single locality anywhere in the world. While the lack of reliable taxonomic revisions in several large and critical genera make an exact count impossible at the present time, it has been estimated that at least 59 genera and 172 species occurred within a few square kilometers in the collection area (see Table I); exhaustive collecting would probably increase the species count to well over 200. This fauna far exceeds those of the better known temperate localities. To cite an example, Dr. Mary Talbot has recorded 22 genera and 67 species in a diversified area of fields and woodland at the Edwin S. George Reserve in southern Michigan. (Talbot, pers. commun.). The Reserve covers 2 square miles, or approximately 5 square kilometers, and is therefore comparable to the area studied at the Busu River. Dr. Talbot considers the fauna at the Reserve to be unusually rich for a locality at this latitude, and her coverage is undoubtedly much more nearly complete than my own at the Busu River. Localities in the southern United States do not harbor notably richer faunas than that at the Edwin S. George Reserve. Van Pelt (1956), for instance, recorded a total of 30 genera and 76 species during a careful survey of the 8-kilometer square Welaka Reserve in central Florida. It is therefore evident that the Busu-Bupu

TABLE I. Composition of three local ant faunas

Genus	Number of Species		
	Lower Busu River, New Guinea	Welaka Reserve, Florida (A. F. Van Pelt)	E. S. George Reserve, Michigan (M. Talbot)
PONERINAE			
Amblyopone	..	1	1
Anochetus	2	..	..
Brachyponera	1	..	..
Cryptopone	2	..	..
Diacamma	1	..	..
Ectomomyrmex	2	..	..
Gnamptogenys	1	..	..
Leptogenys	3	1	.
Mesoponera	1	..	..
Myopias	6	..	.
Odontomachus	3	1	..
Platythyrea	1	..	..
Ponera	6	3	1
Prionopelta	1	..	
Proceratium	..	2	1
Rhytidoponera	3	..	..
Trachymesopus	3	1	..
CERAPACHYINAE			
Cerapachys	4	..	..
DORYLINAE			
Aenictus	2	..	..
Neivamyrmex	..	2	..
PSEUDOMYRMECINAE			
Pseudomyrmex	..	2	..
Tetraponera	3	..	..
MYRMICINAE			
Adelomyrmex	1	..	..
Acidomyrmex	1	..	..
Ancyridris	1	..	..
Aphaenogaster	2	7	4
Cardiocondyla	2	3	.
Crematogaster	6	5	2
Dacetinops	1	..	..
Dilobocondyla	1	..	..
Heptastruma	1	..	..
Kyidris	1	..	.
Leptothorax	..	2	7
Lordomyrma	3	..	.
Meranoplus	1	.	..
Monomorium	1	2	1
Myrmecina	3	1	1
Myrmica	..	..	6
Oligomyrmex	2	..	..
Pheidole	15	6	..
Pheidologeton	1	..	..
Podomyrma	5	..	..
Pogonomyrmex	..	1	..
Pristomyrmex	3	..	..
Rhopalomastix	1	..	..
Rhopalothrix	3	..	.
Smithistruma	..	7	1
Solenopsis	1	6	1
Stenamma	..	..	3
Strumigenys	12	1	..
Tetramorium	..	3	..
Trachymyrmex	..	1	..
Triglyphothrix	1	..	..
Vollenhovia	2	..	..
Xiphomyrmex	1	..	..
Incertae sedis	3	..	..
DOLICHODERINAE			
Conomyrma	..	2	..
Hypoclinea	..	1	4
Iridomyrmex	5	2	..
Leptomyrmex	2	..	..
Tapinoma	..	1	1
Technomyrmex	1	..	..
Tumeria	2	..	..

TABLE I—(Continued)

Genus	Number of Species		
	Lower Busu River, New Guinea	Welaka Reserve, Florida (A. F. Van Pelt)	E. S. George Reserve, Michigan (M. Talbot)
FORMICINAE			
Acanthomyops	..	.	4
Acropyga	3		
Brachymyrmex	..	1	1
Camponotus	8	5	5
Calomyrmex	1	.	..
Echinopla	2		.
Formica	..	3	12
Lasius	..	..	8
Nylanderia	6	2	1
Oecophylla	1		
Opisthopsis	1	..	
Paratrechina	...	1	
Plagiolepis	2		
Polyergus	..	..	1
Polyrhachis	15	..	..
Prenolepis	..	1	1
Pseudolasius	1	..	
TOTAL GENERA	59	30	22
TOTAL SPECIES	172	76	67

area, and other favorable lowland rain forest areas in New Guinea, contain faunas that are larger by a factor of 2 to 4 than those of most comparable local areas in the United States, a comparison that probably extends as well to the temperate zones of Europe and Asia.

Such a comparison of the sizes of local faunas, emphasizing as it does the traditional richness of the faunas of tropical forests, invites further comparisons of a more fundamental nature. Are the larger tropical faunas ecologically more diversified, and if so, in what way, and by how much? Are certain adaptations more marked in the tropical forest, as opposed to the temperate forest, *i.e.*, do a higher percentage of genera and species exhibit them and in a more exaggerated fashion? Has a general "complexity factor," involving an increased number of potential competitors, predators, and nest-food niches, had a demonstrable effect on the evolution of the fauna? In time it is hoped that we can profitably inquire whether a consideration of the adaptation itself, along with the peculiarities of local areal distribution in the rain forest, might not provide a clearer understanding of why tropical rain forests contain such large faunas and have served historically as the centers of major evolution in this group of insects.

Stratification in the Busu River Forest Fauna

Stratification of the fauna is well marked in the Busu forest. While each species is locally distributed in a pattern peculiar to itself, with a high degree of interspecies discordance obtaining, it has been found convenient for purposes of broad description of the ant habitats to recognize three arbitrarily delineated strata. These are characterized in the sections below.

Ground stratum. This division comprises the species that nest in the soil, leaf litter, and all rotting wood on the ground, up to and including the largest rotting logs. The great bulk of both species and individual colonies live here, and relatively few of the species ever leave it to forage in the arboreal zones. On the other hand, a notably larger percentage of true arboreal-nesting species, including such abundant forms as *Iridomyrmex scrutator* (Fr. Smith), *Oecophylla smaragdina* (Fabr.), and *Polyrhachis* (*P.*) *erosispina* Emery commonly forage on the ground to swell the number of species occurring there. As might be expected, the available nesting sites in the ground zone are tremendously varied and the ecology of its resident species far more complex than is the case in the arboreal zones. A more detailed description of this stratum will be given in a later section.

Low arboreal stratum. Including species nesting in herbaceous and shrubby ground vegetation, the C-stratum of trees, and the first several meters of the trunks of larger trees. A small number of species nest primarily or exclusively in this zone: *Diacamma rugosum* (Le Guillou), *Lordomyrma* sp. (891),[3] *Iridomyrmex cordatus* (Fr. Smith), *Calomyrmex laevissimus* (Fr. Smith), *Polyrhachis* (*P.*) *erosispina* Emery, and several species of *Polyrhachis* (*Myrmhopla*). Up into the low arboreal zone come two ground-nesting species to do most or all of their foraging: *Platythyrea parallela* (Fr. Smith) and *Meranoplus spinosus* (Fr. Smith). Some ground-nesting forms are incidental visitors, *e.g. Odontomachus simillimus* (Fr. Smith) and *Tetramorium* spp., while many high-arboreal species descend into the low arboreal zone commonly, *e.g. Podomyrma* spp., *Oecophylla smaragdina* (Fabr.), *Polyrhachis* (*Cyrtomyrma*) spp., and *Camponotus* (*Colobopsis*) *vitreus* (Fr. Smith). This is the most sparsely populated of the 3 zones, with respect to both nesters and incursive foragers.

High arboreal stratum. Including species that nest in the upper trunks and canopy of the A- and B-stratum trees. Within this zone ants nest primarily in epiphytes (*Iridomyrmex scrutator* (Fr. Smith), *Polyrhachis* (*Myrma*) *andromache* Roger, *Camponotus papua* Emery), abandoned termitaria (*Crematogaster* sp. (909). *Camponotus*

[3] Accession numbers are given in those cases where identifications to species cannot be made. They correspond to series on deposit in the insect collections of the Museum of Comparative Zoology.

(*Colobopsis*) (*vitreus*), preformed cavities in live wood (most or all species of *Podomyrma* and at least one undetermined *Iridomyrmex*), and dead twigs (*Turneria* spp.).[4] Many of these species limit their foraging activity to the high arboreal zone (*e.g. Turneria* spp.), while others forage all the way to the ground. One species, an apparently undescribed *Pheidole* (*Pheidolacanthinus*) (accession number 925), nests both in this zone (in tree holes) and in the ground zone (large rotting logs), while appearing to forage exclusively in the arboreal zones. It is unique in this respect among the ants studied.

Further Description of the Ground Stratum

Soil residents. The ground stratum contains 2 distinct major divisions. First can be distinguished the ants that nest in the soil exclusively or extend their nests from the soil into rotting logs. Relatively few rain forest ants nest primarily in the soil. Among these exceptional forms is *Cardiocondyla paradoxa,* which digs to about 20 cm in the earth and constructs a single entrance gallery concealed by leaf litter. *Rhopalothrix biroi* Szabó, on the single occasion a colony was found, was nesting in shallow galleries in the soil beneath a large rotting log. *Acidomyrmex melleus* (Emery) develops enormous colonies that penetrate deep into the soil and heap up massive earthen domes, which are turret- or castle-shaped following recent excavation. *Odontomachus simillimus* (Fr. Smith), *O. papuana* Emery, and species of *Leptomyrmex* nest primarily in the soil, but on occasion colonies have also been found in large logs in a late stage of decomposition. *Acropyga moluccana* Mayr and *Pseudolasius breviceps* Emery are primarily ground dwellers that extend their nests up into late-stage rotting logs. The single colony of *Leptogenys optica* found occupied a similar nest form.

Among ground-nesting ants few species nest or even forage beneath rocks. Only two species, *Cryptopone butteli* Forel and *Pheidole* (*Electropheidole*) *cervicornis* Emery, are found nesting in this situation. Workers of a few species of *Ponera* were found foraging beneath stones, but in each case were more abundant in adjacent open leaf litter. Fewer than 10% of rocks on the floor of the Busu forest had ants nesting or foraging under them. This is in marked contrast to the forests of the temperate regions of the world and in a lesser degree to the montane forests in New Guinea, where stones tend to be the favored nesting sites.[5]

Residents of small pieces of rotting wood. The densest concentration of nesting ants, both in number of colonies and actual biomass, is to be found in small pieces of rotting wood on the ground, at the "zorapteran" and "passalid" stages of decomposition (see below). Included are entire small logs and variously shaped fragments of wood up to approximately 8 cm in diameter Genera that nest primarily or exclusively in this situation include *Ponera, Brachyponera, Prionopelta, Mesoponera, Myopias, Rhytidoponera, Cerapachys, Pheidole, Tetramorium, Xiphomyrmex, Oligomyrmex, Myrmecina, Pristomyrmex, Adelomyrmex, Triglyphothrix, Strumigenys, Kyidris,* and *Dacetinops,* all belonging to the subfamilies Ponerinae, Cerapachyinae, and Myrmicinae.

The prevalence of ponerines, cerapachyines, and myrmicines in small pieces of rotting wood is a conspicuous feature of rain forest ecology and is deserving of further careful study. It appears to the author that there are at least 3 reasons why the nest site might be so favored: (1) the pieces of wood tend to maintain uniform and favorable conditions of temperature and humidity, (2) extensive stable preformed cavities exist, not so likely to be disturbed by burrowing insects and earthworms as galleries excavated in the soil and large logs, (3) a dual habitat for foraging is available, consisting of both the rotting wood and the immediately surrounding soil and leaf litter layer.

Residents of large rotting logs. Logs with diameters greater than approximately 8 cm contain a proportionately light concentration of resident ants, possibly because they are deficient in features (2) and (3) above. The species normally occurring there comprise a fauna well demarcated from the soil and small-log faunas. They tend to confine their foraging to the interior of the logs, rarely venturing out onto the ground or into the arboreal zones. Conversely, non-resident ant species rarely penetrate into the larger logs. Species characteristic of this micro-habitat include *Myopopone castanea* (Fr. Smith), *Trachymesopus stigma* (Fabr.), several small *Pheidole* species, *Solenopsis* (*Diplorhoptrum*) *papuana* Emery, and species of *Vollenhovia.*

A microsere involving the resident ant fauna is well marked in large rotting logs in the Busu forest and other lowland rain forests in New Guinea. In the following sections I have at-

[4] Based on a study conducted on Espiritu Santo, New Hebrides, where *Turneria* are among the dominant ants of the lowland rain forest. At the Busu River these ants were rather scarce, and no nests were found.

[5] This generalization evidently holds for most or all of the tropics. I have found ants relatively scarce under rocks in rain forests in Vera Cruz, Mexico, and Ceylon, while W. L. Brown and A. C. Cole (pers. commun.) have made similar observations in Assam.

tempted a description of this microsere in which 5 arbitrary stages are recognized, each with a significantly different association of ants.

I. "Scolytid stage." The tree has only recently fallen. The wood is no longer "green," but the bark adheres as firmly as to the living tree. Ants are quite scarce, and probably include some species that normally reside in the living tree. No ants were definitely associated with this stage in the Busu forest, but species of *Podomyrma* very likely occupy it to some extent. It has been noted that in the arid eucalyptus woodland of Western Australia *P. adelaidei* (Fr. Smith) frequently nests in abandoned cossid burrows in logs of this stage.

II. "Cucujid stage." The wood is just beginning to rot, and fungal activity is particularly evident under the bark, which can be peeled away in large strips with a knife. Beetle tunnels are common in the subcortical areas, but there are no large frass-filled cavities available for occupation by ants. Ants are nevertheless fairly abundant in whatever cavities exist. Species apparently favoring stage II in the Busu Forest include one of *Pheidole* (933) and two of *Solenopsis* (*Diplorhoptrum*) (931, 1028). In other lowland New Guinea localities species of *Iridomyrmex* and *Nylanderia* are occasionally found here. Although not measured, temperature and moisture within the occupied cavities appear much more variable than in similar cavities in logs at later stages of decomposition.

III. "Zorapteran stage." The wood is considerably softer and can be torn out in large pieces with an ordinary digging tool. The bark is still intact but can easily be pulled off in large pieces to reveal extensive subcortical cavities partly filled with frass. In these cavities abound arthropod groups, including collembolans, mites, isopods, symphylans, campodeids, japygids, and representatives of various beetle families. In New Guinea, zorapterans appear to be limited to logs in this stage of decomposition and are often among the dominant arthropods there. Passalid beetles have begun to infiltrate, but are not nearly so common as in the following (passalid) stage. Ants are extremely abundant and include chiefly *Myopopone castanea* (Fr. Smith), *Trachymesopus stigma* (Fabr.), *Cryptopone motschulskyi* Donisthorpe, *Ponera pruinosa* Emery, and several species of *Vollenhovia* and *Nylanderia*.

IV. "Passalid stage." The wood is thoroughly rotten and can be crumbled easily in the hands, while the bark is fragmenting and sloughing of its own weight. Passalid beetles are among the dominant larger insects. The ant fauna is mostly restricted to several species that also occur in the preceding stage, notably *Ponera pruinosa* and one or two species of *Nylanderia*. The other species characteristic of the zorapteran stage are much less common in the passalid stage and evidently in the process of dropping out. As mentioned already, certain soil-nesting species of *Odontomachus* and *Leptogenys* sometimes occupy passalid-stage logs secondarily, while *Leptogenys optica* may penetrate them from nests located primarily in the soil.

V. "Staphylinid stage." The bark has mostly or entirely fallen off, and the entire log may be covered with moss or herbaceous plants. Wood adjacent to the ground has deteriorated to the point of mingling with the soil. Ants characteristic of the preceding (passalid) stage are no longer present, or at the most occupy large pieces of wood that still approximate the general conditions of that stage. The truly characteristic ants of this stage are species of *Acropyga* and *Pseudolasius* that have extended their nests up from the soil.

Several additional notes on the rotting log habitat must be added here. First, it should be mentioned that small logs, branches, twigs, and other fragments of wood pass through decomposition stages similar to those just described for large logs but much less distinct. Smaller pieces of wood in stages equivalent to III and IV, contain the largest number of resident species of any rain forest microhabitat and probably the highest concentration of individual ants. These wood fragments are especially favored by nesting ants when they are partly or wholly buried in moist, well-aerated leaf litter.

Logs of all sizes are seldom at any given time uniformly in one stage of decay, but rather through differential rates of decay, they form mosaics of wood in several decomposition stages. For example, stage V typically contains sizeable fragments of stage IV wood with its distinctive ant fauna. Moreover, not all species of trees pass through a microsere precisely as described. In some the bark falls off rapidly, before the wood has rotted much, and as a result there is no proper "zorapteran stage." In others the converse is true; the wood rots and begins to crumble before the bark breaks, and large central cavities form. This, incidentally, is the type of log preferred by wood-nesting *Leptomyrmex*, which need spacious preformed chambers.

Further Description of the Arboreal Strata

It is a noteworthy fact that the bulk of the arboricolous ant population nests in preformed cavities in living wood in the forest canopy. Ants

are scarce in small, hollow, dead twigs—only *Technomyrmex albipes,* a species limited to the forest border, is definitely known to use this kind of nest site at the Busu River. In striking contrast is the lowland rain forest fauna studied by the author at Pueblo Nuevo, Veracruz, Mexico, in 1953. Here large numbers of species of *Platythyrea, Pseudomyrmex, Paracryptocerus, Cyathomyrmex, Leptothorax,* and *Camponotus* form dense populations in dead twigs in the low arboreal zone. While exact counts have not been made, there can be little doubt that the arboreal fauna of Pueblo Nuevo, including, in addition to the forms just listed, live-stem dwellers such as *Azteca* and epiphyte dwellers such as *Crematogaster* and *Neoponera,* contains a significantly higher percentage of species (with reference to the total local fauna) than is the case at the Busu River. This relative species paucity in the arboreal fauna extends to all of Melanesia, and is particularly noticeable in the New Caledonian fauna.

A notable feature of the various faunal strata at the Busu River and other lowland localities in New Guinea is the tendency of workers to migrate downward during foraging. (The opposite may be true in other areas, such as New Caledonia). As noted previously, high arboreal species are abundant as foragers in the low arboreal zone and often penetrate to the ground zone, while low arboreal species commonly forage in the ground zone. Yet, despite the fact that the great majority of ant species nest in the ground zone, there is little foraging movement from the ground upwards. Few ground-zone residents forage into the low arboreal zone, and to my knowledge none ever reaches the high arboreal zone. Furthermore, the tendency for migration is extended even to within the ground zone itself. It has been noted that small-log dwellers normally forage out into adjacent soil and leaf litter, but true ground-nesting species are seldom encountered in rotting logs.

The Ecological Distribution of Spinescent Species

During the present study an attempt was made to correlate degree of worker spinescence, *i.e.,* the number and size of spines on the body of the worker caste, with habitat preference or other particularities of behavior. My previous conception, held in common with a few other students of ants, was that conspicuous spinescence is to a degree associated with arboreal life. Actually, no such association was found in the New Guinea rain forests. On the contrary, the high arboreal species are noteworthy for their reduced spination. Two of the 3 known high arboreal myrmicine genera, *Podomyrma* and *Dilobocondyla,* are spineless, while the third genus, *Crematogaster,* has propodeal spines of only moderate size. *Cyrtomyrma,* the dominant of the *Polyrhachis* subgenera in the high arboreal zone with respect to both species and biomass, has greatly reduced spines. All of the other high arboreal species, including members of *Tetraponera, Iridomyrmex, Turneria,* and *Camponotus,* are spineless.

The maximum development of spines is in fact seen in species that nest in the ground and low arboreal zones and forage in the open. Examples of extremely spinescent groups that fit this rule include subgenus *Planimyrma* of *Aphaenogaster,* subgenera *Pheidolacanthinus* and *Electropheidole* of *Pheidole,* and *Ancyridris,* most or all of which nest and forage in the ground zone; *Arnoldidris* and *Polyrhachis* subgenus *Chariomyrma,* which nest primarily in the ground and forage in both the ground and low arboreal zones; and *Polyrhachis* subgenus *Myrmhopla,* which nests and forages almost exclusively in the low arboreal zone. In cryptobiotic ground-dwelling species, *i.e.* those that forage mostly or entirely underground or inside rotting logs, there is a tendency for reduction in spination similar to that seen in the high arboreal forms.

In short, spinescence appears to be associated not with arboreal habits *per se,* but rather with epigaeic foraging behavior. It seems probable that spines serve as a defense against predators and that they are reduced only when confining conditions of the environment such as the cramped quarters occupied by twig-dwelling species or the narrow trophophoric field used by subterranean species, make such armament disadvantageous.

A Preliminary Classification of Food Habits

It is possible to classify the rain forest ants according to their most conspicuous food habit into the following rough categories: (1) specialist predators, (2) general predators, (3) pastoralists, (4) harvesters. By "conspicuous food habit" is meant the special case of what appears, on the basis of usually limited field observations, to be taking up most of the workers' time in food gathering. This is by no means necessarily the only food habit, as will be shown below.

Specialist predators. In the rain forests the following types of specialists were discovered: millipede predators (two undescribed species of *Myopias*), isopod predators (*Leptogenys triloba* Emery), collembolan predators (*Strumigenys*

spp.), predators on small, soft-bodied arthropods (*Rhopalothrix biroi* Szabó, *Strumigenys loriae* Emery),[6] predators on other ants (*Cerapachys opaca* Emery). Many of these ants are marked by peculiarities in mandible structure, which, at least in the case of the *Strumigenys,* has been demonstrated to have a direct relation to specialized hunting behavior. *Strumigenys* workers capture collembolans by striking them and lifting them off the ground with their exceptionally long mandibles. Ant species that are prey-specific are usually also exclusively predaceous, *i.e.,* do not scavenge or gather honeydew in addition. An interesting exception to this rule is the parasitic myrmicine *Kyidris yaleogyna* Wilson and Brown, which, in addition to hunting collembolans and other small arthropods with its host species, *Strumigenys loriae,* also attend coccids (Wilson and Brown 1956).

General predators. This category includes species that accept a wide range of small animals as prey. Their mandibles are not specialized, they frequently appear individually clumsy in the capture of prey, and they often depend in large part on newly eclosed or crippled arthropods. Moreover, many species are secondarily scavengers, readily accepting dead animals as well as rotted or desiccated fragments. Collembolans form a large part of the diet of many of the smaller species. Probably a majority of the genera and species of rain forest ants belong in the general predator category. Examples include most or all of the species of such large and prominent genera as *Rhytidoponera, Ectomomyrmex, Podomyrma, Tetramorium, Xiphomyrmex, Myrmecina, Acidomyrmex, Pheidole,* and *Aphaenogaster* (*Planimyrma*).

Pastoralists. This category comprises the species of *Acropyga* and *Pseudolasius,* which appear to devote most of their time to tending honeydew-secreting insects within the confines of their nests. *Crematogaster* and *Iridomyrmex* may also prove to belong to this category when their habits are better known, but in addition to honeydew these two genera depend in great part on dead insects and could as well be put in a special "scavenger" category.

Harvesters. Ants belonging to this category are relatively scarce in the rain forest. Examples include *Pheidole* (*P.*) sp. (1023) and *Pheidole* (*Pheidolacanthinus*) sp. (1065), both of which have been found with abundant seeds and seed fragments in their nests.

[6] The feeding behavior of these species has been reported on in detail elsewhere (Wilson 1956, 1958c; Wilson and Brown 1956).

Colony Size

In Table II are given estimates of colony size of one to several colonies of rain forest species belonging to a wide range of ant groups. These data represent rough counts of the adult workers, taken to the nearest 5 in populations of 30 or less, to the nearest 10 for populations between 30 and 200, and to the nearest 50, 100 or 1000 for populations of increasingly larger size. Care was taken to avoid incipient colonies and colony fragments. In nearly every case the mother queen was uncovered, and the workers were full-sized (nonnanitic). The estimates given, although representing either unique colonies or at most very limited samples, nevertheless in most cases probably do not deviate far from the actual species averages, since an attempt was made to choose typical nests or relatively common species on which repeated subjective estimates were made.

On the basis of these limited quantitative data, plus a much wider range of subjective impressions, a few preliminary generalizations can be drawn. Perhaps the most important is that most rain forest species have small to moderate-sized colonies. Colony populations do not often contain more than several hundred adult individuals, while mature colonies of less than 50 adults are common and typify many species.

In general, ponerines, cerapachyines, and myrmicines maintain smaller colonies than dolichoderines and formicines, a fact that has already been noted by past authors in other parts of the world. Arboricolous species tend to maintain larger colonies than terricolous ones, but this is of course partly a function of the greater concentration of formicines and dolichoderines in the arboreal zones.

Perhaps the most important single ultimate factor regulating colony size in the rain forest is limitation of nest space. As previously noted, the greatest number of species nest in small pieces of rotting wood on the ground, and are further limited to wood fragments in intermediate stages of decomposition. Unless the colony is dispersed through several wood fragments, which is exceptional, it is clear that its total size can be limited by living space alone. It would seem to be of considerable adaptive advantage for species living in this situation to control colony size and to

TABLE II. Estimated nest population of selected species

Species	Locality	Accession number	Estimated adult population size
PONERINAE			
Prionopelta opaca Emery	Karema	595	20
Platythyrea parallela (Fr. Smith)	"	570	50
Rhytidoponera araneoides (Le Guillou)	"	3 accessions	50
R. laciniosa Viehmeyer	Busu R.	1002,1031	100,150
Gnamptogenys macretes Brown	Bisianumu	649	40
Leptogenys bituberculata Emery	"	663	300
L. diminuta (Fr. Smith)	Karema, Bisianumu, Nadzab	539,608,1087,1106	90–400
L. purpurea Emery	Tumnang	803,849	500,2000
Mesoponera papuana Viehmeyer	Busu R.	994	10
Diacamma rugosum (Le Guillou)	Nadzab, Didiman Creek	2 accessions	30,50
Cryptopone motschulskyi Donisthorpe	Bisianumu	626	20
Ectomomyrmex striatulus Karawajew	Karema, Wamuki	532,857	10,20
Myopias concava Willey and Brown	Busu R.	990	60
M. julivora Willey and Brown	"	905,1048	40,70
M. sp.	"	983	30
CERAPACHYINAE			
Cerapachys opaca Emery	Busu R.	921	100
C. *polynikes* Wilson	"	936	20
DORYLINAE			
Aenictus currax Emery	Karema	562	100,000+
MYRMICINAE			
Cardiocondyla thoracica (Fr. Smith)	Bisianumu	653	70
C. paradoxa Emery	Didiman Creek	703	50
Crematogaster (Orthocrema) *elegans* (Fr. Smith)	"	692	300
Cr. (Acrocoelia) *subtilis* Viehmeyer	Busu R.	909	5000+
Cr. (Acrocoelia) sp.	"	910	300+
Strumigenys bajarii Brown	Busu R.	969	400
S. frivaldszkyi Emery	Karema	594	15
S. mayri Emery	Bandong	1125	100
S. loriai Emery	Bubia, Busu R.	686,907	300,500
S. sp.	Busu R.	926	200
S. sp.	"	1008	50
Rhopalothrix biroi Szabó	"	987	50
Dacetinops cibdela Brown and Wilson	"	1058	10
Ancyridris sp.	"	956,973	10,15
Podomyrma sp.	"	1055	200+
Pristomyrmex sp.	Nadzab	1083	100
Adelomyrmex biroi Emery	Busu R.	935	10
Acidomyrmex melleus Emery	Bisianumu, Tumnang	2 accessions	5000+
Vollenhovia brachycera Emery	Karema	567	150
Aphaenogaster (Planimyrma) dromedarius Emery	Busu R.	908	100
Myrmecina transversa Emery	"	875	50
Meranoplus spinosus (Fr. Smith)	Ebabaang	821	150
Pheidole (Pheidole) sp.	Busu R.	1023	50
Pheidole (Pheidolacanthinus) spp. (several)	"		50–200
Pheidologeton sp.	Karema	591	3000+
P. sp.	Busu R.	874	5000+
DOLICHODERINAE			
Leptomyrmex *fragilis* (Fr. Smith)	Bubia	1061	350
Iridomyrmex scrutator (Fr. Smith)	Busu R.	several accessions	500–3000+
FORMICINAE			
Pseudolasius breviceps Emery	Karema	543,547	500,200
Acropyga sp.	Busu R.	906	1000+
Paratrechina (Paraparatrechina) pallida Donisthorpe	Bubia	684	500
Paratrechina (Nylanderia) sp.	Busu R.	972	200
P. (N.) sp.	"	1038	150
Camponotus papua Emery	Nadzab	1095	300
C. confusus Emery	Bisianumu	620	200
C. vitreus (Fr. Smith)	Busu R.	881	4000+
Calomyrmex laevissimus (Fr. Smith)	Bisianumu	609	250
Polyrhachis (Chariomyrma) hirsutula Emery	Bisianumu	629	150
P. (Chariomyrma) limbata Emery	Busu R.	937	100
P. (Chariomyrma) sp.	Bisianumu	605	30
P. (Cyrtomyrma) debilis Emery	Karema, Bubia, Bisianumu	556,603,1077	300–350
P. (Myrma) rufiventris Emery	Karema	586	200
P. (Myrmatopa) omyrmex (Donisthorpe)	Busu R.	1014	60

achieve the ability to rear through sexual broods with a small worker force.[7]

Beyond the immediate association between nest site and colony size, it seems safe to generalize that specialist predators tend to have the smallest colonies, while the largest colonies are formed by species that derive a large part of their diet from insect honeydew. This would seem on first examination to be a function of diversity and local abundance of food supply. Legionary species, *e.g. Aenictus* spp. and *Leptogenys purpurea* Emery, are exceptional in being able to maintain large colonies, since, despite their exclusively predatory habits, they are constantly shifting hunting grounds (Wilson 1958b).

Among the many rain forest species studied, monogyny appears to be the strong rule. In the exceptional cases where multiple queens are present, they rarely exceed 2 or 3 per colony. In the great majority of species the brood is not synchronized in its development, *i.e.,* it is spread at any given moment over most or all of the developmental stages, and there is no evidence for marked periodicity of oviposition. Notable exceptions include the legionary species just mentioned in the genera *Aenictus* and *Leptogenys*.

[7] The tendency for rain forest ants to nest in small pieces of rotting wood and the effects of this habitat choice on colony size, phenomena also noted by the author in tropical rain forests in other parts of the world (Ceylon, Mexico), have some important evolutionary implications. There is growing evidence at the present time to suggest that tropical rain forests, particularly those in the central continental areas of the Old World, are the chief evolutionary centers for most ant groups. Certainly at the present time the tropical rain forests, both in the Old and New Worlds, contain the highest concentration of species and basic phylogenetic stocks of any of the major vegetation zones. Wheeler's well known (1928) statements concerning the primary importance of desert regions are no longer supported by modern zoogeographic evidence. (cf. Bernard 1953, Kusnezov 1957). Under such circumstances the great favorability of the small-log habitat must have had considerable influence on the course of evolution of the ponerines and myrmicines. Moreover, it very probably played an important role in the early evolution of the Dolichoderinae and Formicinae, since it has recently been shown that *Aneuretus simoni* Emery, the sole living member of the related, primitive subfamily Aneuretinae, normally forms small colonies in fragments of rotting wood on the floor of rain forest (Wilson *et al.* 1956). A hypothesis worth considering is that many, perhaps most, of the phyletic groups of ponerines and myrmicines have passed through an evolutionary stage in which they were adapted primarily to life in the small-log habitat in tropical rain forests, and that, in radiating and penetrating new habitats, they have tended to conserve the modest colony size that characterizes most of these groups today. There is good evidence, on the other hand, to suggest that the small-log habitat is not primitive for ants generally. The most primitive subfamily of ants, the Myrmeciinae, represented by two genera limited to Australia and New Caledonia, consists in large part of soil dwelling species that frequently form large colonies containing thousands of workers.

Discussion: Ecological Diversification in the Rain Forest Fauna

Considering the great taxonomic and distributional complexity of the New Guinea ant fauna, one is inclined to ask, to what extent is there a correlated ecological diversification? There are two aspects of such diversification that must be examined separately. First is the question of the maximum ecological amplitude attained by the fauna as a whole. Surprisingly, the New Guinea fauna does not at first glance appear to have much greater amplitude than a temperate fauna such as that studied by Van Pelt (1956) in Central Florida. In both areas are found, among others, extreme specialists, including exclusively arboricolous forms, army ants, collembolan-feeders and subterranean coccid tenders. Each area contains remarkable specialists the other lacks: New Guinea has myrmecophagous forms (Cerapachyinae), while Florida has fungus growers (Attini). In a north temperate zone, such as Dr. Talbot's study area in Livingston County, Michigan, the fauna appears to have fewer extreme specialists, but the difference is not great. There are arboricolous species, collembolan-feeders, subterranean coccid-tenders, and an impressive array of other major adaptive types in both areas. In the case of the Floridian fauna, it is true that many of the principal adaptive forms probably originated in forest centers in the Neotropical Region rather than in the Old World. However, this does not affect the main argument that many or most of the major adaptive types found in the New Guinea rain forests thrive in this temperate area as well. The comparison has not been carefully extended, as it should be, to the Neotropical rain forests, but there is abundant evidence in the literature on the Neotropical fauna to show that the generalization holds if the New World alone were considered.

But such forms of comparison, based simply on an enumeration of major adaptive types, can be misleading. The true distinction of the rain forest fauna appears to me to lie in the fact that its species have not only invaded principal niches, but saturated them as well. The arboricolous fauna can be considered typical in this regard. In central Florida a small number of species (16 according to Van Pelt) nest arboreally; these are confined almost entirely to dead hollow stems and favorable crevices in tree trunks. In the Lae area of New Guinea the arboricolous fauna is several times as large. Its specialized species live in a great variety of arboreal situations: live plant stems, dead stems, myrmecophyte pseudobulbs,

leaves bound together with silk, carton nests on leaves, and silken nests woven on the sides of tree trunks. The total arboricolous ant populations are, moreover, much denser in the New Guinea rain forests. The same considerations hold in even greater measure with respect to the Neotropical arboricolous fauna, which is phylogenetically closer to the Floridian fauna and hence more appropriate for such a comparison.

Local tropical ant faunas are usually adaptively more diversified and contain a larger number of species than local temperate faunas. Our information is not adequate to determine whether individual species in these faunas tend to be more specialized, but it is certain, and perhaps more significant, that a greater number of specialists coexist at any given time. This continuing richness is the source of the evolutionary vitality that characterizes tropical faunas. It can be conjectured that as a rule successful new major adaptive types of ants originate and achieve initial radiation in the tropical rain forests. If this is true, a "generally adapted" ant group would usually be one that has been notably successful in the tropical rain forests and hence is more likely to produce species that can penetrate adjacent temperate and arid regions secondarily.

Summary

1. Local ant faunas in the lowland rain forests of New Guinea are among the richest in the world and contain approximately 2 to 4 times as many species as faunas occupying comparable areas in north temperate zones.

2. The largest number of species and colonies nest and forage exclusively in the ground zone (soil, leaf litter, and rotting wood on the ground). A smaller number nest in the forest canopy, while a third, still smaller faunal component is restricted primarily to the "low arboreal" zone, including C-stratum trees and the lower trunks of larger trees. Foraging tends to be downward: ground-zone species rarely leave the ground, while low—arboreal species commonly forage on the ground as well as in their own zone, and high-arboreal species often utilize all 3 zones.

3. Most terricolous species nest in small pieces of rotting wood, not exceeding 8 cm in diameter. A smaller but distinctive fauna inhabits larger rotting logs and stumps. True soil-nesting species are relatively scarce in the lowland forests but abundant in the mid-mountain forests above 1000 meters.

4. A rotting-log microsere is well marked in the resident ant species. The greatest concentration of species and colonies occurs in an intermediate ("zorapteran") stage of decomposition, during which there is an abundance of frass-filled cavities beneath a firm covering bark.

5. Worker spinescence is best developed in those species that nest in the ground and low arboreal zones and forage a great deal above ground. High-arboreal and subterranean species are notably non-spinescent, a trait presumably associated with the cramping conditions of their favored nest sites of trophophoric fields.

6. A preliminary classification of food habits is offered. The largest number of species and colonies appear to be general predators, accepting a wide variety of small animals (mostly arthropods) as prey. Specialist predators, pastoralists, and harvesters also occur but are less prominent.

7. Estimates of colony size of selected species are given. Colonies are generally small, usually containing no more than several hundred adults and often as few as 50 or less. This phenomenon seems at least in part to be associated with the generally confining nature of rain forest nest sites.

References

Bernard, F. 1953. Les Fourmis du Tassili des Ajjer (Sahara Central) Publ. Inst. Recherches Sahariennes, Univ. d'Alger.

Brown, W. L. 1958. Contribution toward a reclassification of the Formicidae. II. Tribe Ectatommini. Bull. Mus. Comp. Zool. Harvard **118**: 175-362.

———, and **E. O. Wilson.** 1957. *Dacetinops,* a new ant genus from New Guinea. Breviora **77**: 1-7.

Dahl, F. 1901. Formiciden aus dem Bismarck-Archipel. Mitt. Zool. Mus. Berlin **2**: 1-70.

Kusnezov, N. 1957. Number of ants in faunae of different latitudes. Evolution **11**: 298-299.

Van Pelt, A. F. 1956. The ecology of the ants of the Welaka Reserve, Florida (Hymenoptera: Formicidae). Amer. Midl. Nat. **56**: 358-387.

Wheeler, W. M. 1928. The social insects. New York, Harcourt, Brace.

Wilson, E. O. 1956. Feeding behavior in the ant *Rhopalothrix biroi* Szabó. Psyche **63**: 21-23.

———. 1957a. The *tenuis* and *selenophora* groups of the ant genus *Ponera* (Hymenoptera: Formicidae). Bull. Mus. Comp. Zool. Harvard **116**: 355-386.

———. 1957b. The discovery of cerapachyine ants on New Caledonia, with the description of new species of *Phyracaces* and *Sphinctomyrmex*. Breviora **74**: 1-9.

———. 1958a. Studies on the ant fauna of Melanesia. I. The tribe Leptogenyini. II. The tribes Amblyoponini and Platythyreini. III. *Rhytidoponera* in western Melanesia and the Moluccas. IV. The tribe Ponerini. V. The tribe Odontomachini. Bull. Mus. Comp. Zool. Harvard **118**: 101-153, **119**: 303-371, **120**: 483-510.

———. 1958b. The beginnings of nomadic and group-predatory behavior in the ponerine ants. Evolution **12**: 24-32.

———. 1958c. Observations on the behavior of the cerapachyine ants. Insectes Sociaux 5: 129-140.

———. 1959. Adaptive shift and dispersal in a tropical ant fauna. Evolution 13: 122-144.

Wilson, E. O. and **W. L. Brown.** 1956. New parasitic ants of the genus *Kyidris*, with notes on ecology and behavior. Insectes Sociaux 3: 439-454.

Wilson, E. O., T. Eisner, G. C. Wheeler, and **J. Wheeler.** 1956. *Aneuretus simoni* Emery, a major link in ant evolution. Bull. Mus. Comp. Zool. Harvard 115: 81-99.

FIT OF CERTAIN DISTRIBUTION FUNCTIONS TO COUNTS OF TWO SPECIES OF CRYPTOZOA

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Introduction

The problem of finding mathematical functions capable of describing observed distributions of plants and animals dates at least from a publication of "Student" (1907). This paper was confined to laboratory problems and was not extended to analysis of natural populations. Since "Student," much work has been done, but to date no widely accepted solutions have been attained. The present paper is limited to assaying the worth of some of the theories which have been advanced, and to estimating the fidelity with which distributions calculated from theory fit the observed data.

The term "distribution" is used in this paper to mean the spatial occurrence of one species of animal throughout a certain area on which the animal has been counted by some sampling method. The results of a series of samples are tabulated in the form of a frequency distribution giving the number of samples containing 0, 1, 2, etc. specimens of the animal being counted. "Distribution" is also used to mean the placing of animals in geographic areas or in relation to other objects in the environment, but will not be used in this way here.

The censuses analyzed below are all based on counts of animals classified as members of the cryptozoa, the assemblage of small terrestrial animals dwelling beneath objects lying on the surface of the ground. Cole (1946a) has discussed the origins of the term cryptozoa and has reviewed the literature concerned with the taxonomic categories found in this habitat.

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Procedures

Distributions used in this paper

Theories of distribution intended for use in ecological problems have been developed by numerous people, but of these, this paper investigates only the Polya (1931), the Neyman A (1939), and the negative binomial (or Pascal distribution). The importance of this type of description has been attested to by (among others) Skellam (1952), who points out that census distributions "contribute to the understanding of aspects of the pattern of arrangement of individuals in space" and further "provide estimates of the density of individuals in the region sampled together with information on the reliability of the estimates." The value of this approach is obvious when one considers that population size is a datum significant not only in ecology (Cole 1946b, Anscombe 1950) but also in evolution (Li 1948, Wright 1938) and economic biology (Beall 1935, 1940). The problem can be attacked by marking methods (Jackson 1939), but the use of distribution functions may have certain advantages even where marking is possible. First of all, this approach to the problem may provide parameters interpretable in biological terms. Also, provided that a suitable distribution(s) can be found, appropriate transformations for purposes of standard statistical analyses would be more apparent and less questionable (Fisher 1950, Bliss 1953, Cole 1946a).

Of the functions used in this paper, the negative binomial has been, perhaps, most studied. Bliss (1953) points out that there are at least two kinds of assumptions which lead to the negative binomial. One, if the data are composed of a mixture of Poisson distributions, then the resulting distribution will be a negative binomial; two, if there is real contagion, *i.e.*, if the presence of one individual increases the probability of a second individual in the sample (suggested originally by

"Student" 1919), then this very same distribution may arise again. This latter postulate can also lead to the Polya (1931) distribution. Either of the above functions can be derived by assuming environmental heterogeneity (Greenwood and Yule 1928, Skellam 1952). Derivations of both functions can be found in Feller (1950).

The third distribution studied is that developed by Neyman (1939). This theory has postulates (randomly distributed groups, with members of groups dispersing independently into the surrounding area) which are likely not to be realized in the censuses available; nevertheless it seemed worthwhile to test this theory in the hope that some degree of fit might be observed, as was found by Beall (1940) for more suitable data. Neyman (1939) noted that, if such a fit (to data not embodying his postulates) should occur, it would be a fortunate by-product of his derivation.

All of the above functions have uses other than those touched upon in this paper. In particular, the fitted negative binomial is often used to obtain transformations so that data may be treated by analysis of variance.

Another function tested is that of Cole (1946b), who developed his ideas on the basis of observations that animals form sexual pairs, family groups, and social groups of various sizes. Cole assumes that a particular group size (*e.g.*, pairs) is distributed at random and that the various group distributions may be added. This theory is not on a sound deductive basis and, therefore, cannot be tested by χ^2 or other methods; nevertheless, it has some important effects on the shape of the distribution and will consequently be compared subjectively with the data.

Sources of data—area studied

The data for this paper were all obtained on a farm pasture about 7 miles to the east of Cazenovia, New York, as a by-product of a practical agricultural control problem. The sampling methods used in the control problem have been described in detail elsewhere (Jensen *et al.* 1955). Briefly, the technique was to distribute boards at random on the pasture and then to remove grass and herbage from beneath each board, thus providing a favorable area for counting.

In order to obtain homogeneous data, records of weather factors were maintained and, subsequently, used to combine the data according to the similarity of these environmental agents. Such compilations consist, of course, of a variable number of separate censuses.

Methods of fitting

The negative binomial is fitted according to the technique described by Bliss (1953). This function has two parameters: m, estimated efficiently by the arithmetic mean, $\bar{x}$; and k, estimated by Fisher's (1953) maximum likelihood method which involves finding the value of k for which the equation

$$\Sigma\left(\frac{Ax}{K+x}\right) = N\ln\left(1+\frac{\bar{x}}{k}\right)$$

where ln denotes the natural logarithm and Ax the accumulated frequency in all units with more than x organisms.

The Neyman A is fitted according to the method developed by Beall (1940). This function has two parameters m_1 and m_2, estimated respectively by $m_1 = \mu'_1{}^2/\mu_2 - \mu_1$ and $m_2 = \mu_2 - \mu'^1/\mu'_1$. Although the function exists in a three parameter form, the present discussion will be limited to the two parameter model. The method of fitting given above (by use of moments) is slightly less efficient than the techniques used for the other functions.

The Polya distribution is also characterized by two parameters: m, efficiently estimated by the arithmetic mean; and a, calculated from the mean and the proportion of zero frequencies,

$$a = \frac{2m}{\ln(N/No)} - 2$$

The method of fitting is to be found in an article by Evans (1953).

Cole's theory (1946b) can be fitted by two techniques. In this paper, the method most frequently used is to solve for group means by the use of simultaneous equations. Occasional use is made of a second method, *i.e.*, each group mean is calculated separately. For further information on methods of fitting, the reader is referred to the above mentioned papers, particularly to Evans (1953), who describes techniques of fitting for each of the three functions.

The Data

From the mass of data obtained in the field, a large number of distributions were obtained. These distributions show a wide range in form and, therefore, both typical and atypical examples are included in the tables below. Table I shows a characteristic distribution. At the top of this table is a statement as to the kind of environment from which the censuses were compiled, along with the mean $\bar{x}$ and the variance V of the distribution. The first column shows the number of snails per sample and the second column the number of samples. NB designates the negative binomial, NA the Neyman A. The names Cole and

Polya represent their respective distributions. At the bottom of each column is the P (probability) value for the difference between calculated and observed frequencies as measured by χ^2. Beneath the P values are the estimates of the parameters (rounded to four decimal places) used to fit the distributions. The m statistics given beneath Cole's distributions are means, and have a subscript designating the group size.

TABLE I. *C. lubrica*. Undisturbed plots, 1953. $\bar{x} = .9106$, $V = 1.8111$

Number of individuals	Number of samples	NB	NA	Polya	Cole
0	240	247.03	269.77	240.00	240.00
1	144	124.04	91.38	127.39	144.00
2	56	58.96	60.66	63.94	56.00
3	13	27.50	31.94	29.10	16.32
4	12	12.70	15.25	12.40	13.99
5	8				5.01
6	5				
7	0	9.77	11.00	7.17	4.68
8	1				
10	1				
	480	.001<P<.01	P<.001	.01<P<.02	
Parameter estimates		k=1.1194	m_1=.9208	a=.6196	m_1=.6000
		$\bar{x}$= .9106	m_2=.9889	$\bar{x}$=.9106	m_2=.0533
					m_4=.0291

Table I is fairly typical of the data obtained for the snail, *Cionella lubrica* Müller. The censuses included are heterogeneous for many environmental factors such as temperature and humidity, but come from plots of ground not subjected to any agricultural treatments. The χ^2 test indicates that all of the functions differ significantly from the observed distribution. The negative binomial and Neyman A overestimate the zero frequency, while the Polya and Cole distributions are exactly correct as their methods of fitting require. All of the functions, except Cole's, grossly underestimate the number of individuals at one snail per sample. All over-predict the frequency at 3 snails per sample by a large margin. The Cole distribution is fitted with the aid of 3 group means, each of which is estimated separately (not by solution of simultaneous equations). Cole's theory does show a much improved estimate of the frequency at 3 snails per sample.

Results similar to those shown in Table I are fairly frequent in a large series of distributions of *C. lubrica* obtained in the summers of 1953 and 1954. When fitted with the above functions, like deviations from expectation were often found. To illustrate this point, Table II has been compiled to summarize the probabilities obtained for fitted distributions of *C. lubrica* for the summers 1953-1954. It can be seen that the calculated Neyman A differs significantly from the observed in 4 of 10 cases (1953) and gives relatively poor results in 2 of the remaining 6. Table III further confirms the discrepancy between observed and calculated results for the Neyman A. This table itemizes the χ^2 totals for the frequency distributions of Table II (1953 only). Comparison of the total χ^2 under NA with the totals for the other distributions leads to the conclusion that the Neyman A is not suited to the description of the manner in which *C. lubrica* is spread out in space.

TABLE II. Probability values for the distributions of *C. lubrica* for the summers of 1953-1954

PART A. Environmental factors heterogeneous.

Distribution number	Number of samples	NB	NA	Polya
1953				
1	480	.01<P<.02	P<.001	P<.001
2	120	.05<P<.1	P<.001	.02<P<.05
3	120	.7 <P<.8	.5 <P<.7	.8 <P<.9
4	120	.5 <P<.7	.5 <P<.7	.5 <P<.7
5	120	.3 <P<.5	.2 <P<.3	.2 <P<.3
1954				
1	240	.3 <P<.5	.05<P<.1	.3 <P<.5
2	156	.3 <P<.5	.3 <P<.5	.7 <P<.8
3	84	.2 <P<.3	.7 <P<.8	.3 <P<.5

PART B. Environmental factors homogeneous.

1953				
1	120	.1 <P<.2	.02<P<.05	.1 <P<.2
2	60	.2 <P<.3	.05<P<.1	.5 <P<.7
3	80	.5 <P<.7	P<.001	.3 <P<.5
4	60	.2 <P<.3	.1 <P<.2	.5 <P<.7
5	80	.3 <P<.5	.5 <P<.7	.9 <P<.95
1954				
1	60	.7 <P<.8	.5 <P<.7	.9 <P<.95
2	48	.1 <P<.2	.1 <P<.2	.2 <P<.3
3	48	.9 <P<.95	.8 <P<.9	.3 <P<.5

Tables II and III are divided into 2 sections, an upper portion containing those distributions composed of censuses involving varying environmental factors, and a lower part with distributions based on more homogeneous data. If comparison is made between the 2 sections for the 1953 distributions, a tendency toward a better fit of calculated to observed distribution will be apparent in the latter. For example, in Table II, the calculated negative binomial differs significantly from the observed in one of the 5 distributions in the upper heterogeneous section (and has a poor fit in one other case), but differs not at all in those which are homogeneous. A scanning of the tables will show that this tendency is true for the other functions. Table III confirms the previous rejection of the Neyman A as adequate to describe these distributions. Comparison of the heterogeneous and homogeneous sections of this table

TABLE III. χ^2 totals at each level of the frequency distribution as obtained from distributions fitted to data from undisturbed areas (1953)

PART A. Environmental factors heterogeneous.

Number of C. lubrica	Negative Binomial: Total χ^2	Negative Binomial: Av χ^2 per fitted curve	Neyman A: Total χ^2	Neyman A: Av χ^2 per fitted curve	Polya: Total χ^2	Polya: Av χ^2 per fitted curve
0	.10	.02	1.36	.34		
1	2.25	.56	18.37	4.59	2.33	.58
2	2.96	.74	2.47	.62	3.46	.86
3	6.79	1 70	7.74	1.94	6.73	1.68
4	.47	.47	.....	....	.13	.13
5	4.60	4 60	.....	....	1.64	1.64
remainder	.85		2.51		1.36	
total	18.02		32.45		15 65	

PART B. Environmental factors homogeneous.

0	.27	.05	2.47	.49	.....	
1	3.63	.73	24.36	4 87	1.87	.37
2	.75	.15	.94	.19	1.03	.21
3	8.31	1.66	12.23	2.45	9.82	1.96
remainder	3.96	.99	1.38	.34	3.33	.83
total	16.92		41.38		16 05	

reveals: (a) that the elements of the frequency distributions are about equally well fitted at 0 and 2 in both sections, and (b) that the goodness of fit is poorer at 1 and 3. When these data were further analyzed to show the frequency of overestimation or underestimation for each element of the distribution, the above results were verified. For example, both the negative binomial and the Polya distributions consistently over-predicted the frequency at 2 snails per sample.

In the summer of 1954, more data on *C. lubrica* were obtained and fitted with approximately the same result. In addition, there were a number of highly skewed distributions. All of the functions differed significantly from the latter, which were taken, however, from surfaces which had been subjected to plowing and which were, therefore, presumably less favorable environments. It is probable that under the greater environmental stress produced as a consequence of plowing, the snails would tend to move under boards, thus producing the observed skewness. This is presumably true, but would also occur with any environmental stress. Every distribution must show such effects in some way. We shall return to this question in the discussion.

A second species, the sowbug, *Trachelipus rathkei,* was censused in both summers. This crustacean showed characteristically highly skewed distributions produced by the usual presence of mating pairs, family groups, social aggregations, and aggregations due to environmental stress. A typical set of data is shown in Table IV. The fitted Neyman A, although having a second mode, has this in the wrong position. Such bimodality was frequently found in the *T. rathkei* distributions, but in no case was this second mode, or, for that matter, the entire distribution, adequately described by the Neyman A. The other two functions frequently fitted the data very well according to χ^2 values but did not represent the second mode. The second mode was produced by family groups, while the long tail to the distribution represents the effects of sociality and reaction to environmental factors.

TABLE IV. *Trachelipus rathkei.* Census totals from one area, homogeneous for time of day. $\bar{x} = 3.0714$, $V = 14.0520$

Number of sowbugs	Number of samples	NB	NA	Polya
0	41	40.00	60.74	41.00
1	23	25.11	5.22	20.13
2	17	17.87	9.57	17.00
3	18	13.22	11.94	13.97
4	7	9.96	11.66	11.23
5	5	7.59	9.79	8.87
6	5	5.83	7.63	6.90
7	3	7.98	10.33	9.29
8	11			
9	4			
10	1			
12	1			
15	1	12.44	33.12	11.61
17	1			
18	1			
19	1			
	140	$.2<P<.3$	$P<.001$	$.3<P<.5$
Parameter estimates		$k = .7889$	$m_1 = .8591$	$a = 3.0020$
		$\bar{x} = 3.0714$	$m_2 = 3.5751$	$\bar{x} = 3.0714$

DISCUSSION

The data presented in the preceding section should make obvious the difficulty of deciding which of a number of functions do not describe a distribution and, conversely, which of those tested do give good descriptions. Skellam (1952) has pointed out that, for the above desiderata, it is necessary to obtain data from other sources. That this is true of all theories is self-evident and taken for granted in weighing the validity of such theories. There is, however, a tendency to favor that function among those tested which manages best to survive a battery of statistical tests. Skellam (1952) suggests that more information about the appropriateness of a function could be obtained by studying the relationships between numbers in nearby squares, and by measuring the distances between individuals and their neighbors.

This paper adds to Skellam's list a minute examination of the χ^2 totals at each element of the frequency distribution, an examination of the frequency with which the observed values deviate from the theoretical, a study of the calculated distribution in relation to the underlying biological facts and, lastly, a comparison of the fit of distributions compiled from heterogeneous to those obtained from homogeneous data.

Evans (1953) and Bliss (1953) have both studied some of the functions fitted in this paper. Bliss concluded that the negative binomial was the "most widely adaptable and generally useful of those [functions] that have been proposed so far." Evans is somewhat less definite but favors the negative binomial for insect distributions and the Neyman A for plant distributions. Both authors have utilized data available in the literature. Evans uses a technique of testing developed by Anscombe (1952), a method based on the comparison of certain statistics to their respective standard errors. Evans states that these statistics are equivalent to testing of the over-predictions or under-predictions at an element of the frequency distribution (as has been done in this paper). Evans' statistics test all the frequencies at one time and do not isolate particular elements as has been done here.

Recently McGuire *et al.* (1957) have demonstrated empirically, in fitting distributions of the European corn borer, that the Poisson binomial gave good fits to distributions with low densities of the corn borer while the negative binomial was more suitable at high densities. The Poisson binomial has not been studied here.

The most thorough analysis in this paper is that of the distribution of *C. lubrica*. Since significant differences of calculated from observed distributions were obtained in 6 of 15 distributions of 1953, and 6 of 12 of 1954, the conclusion is made that the Neyman A was not suited to description of the surface spread of this species. This conclusion is confirmed by the consistent lack of agreement between observed and calculated at certain elements of the frequency distribution.

The Neyman A was no more suitable to describe the *T. rathkei* distributions, most of which differed significantly from the calculated. One further argument against this function is the biological observation that modes due to groups of offspring and mating pairs were present in the distributions of *T. rathkei* (and also in distributions of a number of other species not listed). These modes were not shown by any of the functions.

Very likely the Neyman A may be useful in special cases where the underlying assumptions are met. Beall and Rescia (1953) have shown that the Neyman A, B, C are members of a large family of functions. No attempt was made to fit these latter to data in this paper, but, so far as subjective judgment can determine, none would be any more suitable than is the Neyman A. Evans (1953) lists a second method of fitting the Neyman A, but it is unlikely that this technique of fitting would overcome the above arguments.

The other 2 functions used in this paper do not give nearly as clear-cut results as does the Neyman A. Both show a marked similarity in the type of fit produced, and, in fact, part of the differences in fit may be attributed to the different methods of fitting. Both showed a definite discrepancy between observed and calculated frequencies at one, 3, and 5 individuals per sample (*C. lubrica*). This disagreement is apparent in data derived from heterogeneous and homogeneous censuses, but is, in general, larger in the former. This curious fact is difficult to interpret, but on the assumption that the appropriate distributions are best represented by the more homogeneous data, one may conclude that neither function describes the data.

The fourth distribution used is that of Cole (1946b). Where fitted to the *C. lubrica* data, this function has usually given better estimates of the observed frequencies than any of the others. In many cases, this distribution would have required many group sizes and therefore was not fitted. The group size 2 was needed in only a few cases, probably a consequence of the fact that this snail is a spring breeder (Pilsbry 1948) (the snail is possibly a fall breeder also). Cole's theory tacitly assumes a uniform environment since it is postulated that each group size is randomly distributed. The present data have not been taken from any such environment. In general, one can assume environmental heterogeneity and, therefore, anticipate contagion due to this cause. Cole's is the only function taking account of the factors of mating, reproductive groups and sociality. Since we know that there are no mating pairs or reproductive groups of *C. lubrica* during the summer, the only groups to be anticipated are m_1 groups (individuals) and social groups about which nothing is known except that this species sometimes forms large aggregations in the fall (Pilsbry 1948). The data provide no evidence of any one social group size.

The distributions of *T. rathkei* are of particular interest because of their extreme skewness. The Neyman A clearly did not fit these distributions, while the negative binomial differed significantly from one of 8 distributions, and the Polya from 2

of the same 8. The χ^2 values again suggest a bias toward certain members of the frequency distribution. These facts, together with the presence of a second mode due to offspring groups, seem to rule against both these functions. In addition, many copulating pairs were observed, and data for this species show a large χ^2 total at this element of the frequency distribution.

The problem of sample size was not actively pursued in this research due to the press of other duties. This problem is not a question, as has been suggested, of comparing distributions based on varying sample sizes, but one of emulating natural sample sizes. With cryptozoic forms, choice of sample size is governed by naturally occurring cover. Unfortunately the animals studied in this paper are not completely restricted to the cryptozoic habitat. Sample size then must depend on the range of the animal, its sociality, and the rapidity with which topographic variation occurs within the area. Romell (1930) has suggested that any distribution can be made to appear random by use of appropriate sample size. This, however, ignores the occurrence of topographic variation which often delimits demes in a natural way.

No population sizes have been calculated since, as Cole (1946a) pointed out, estimates of population size of contagiously distributed organisms will most of the time be less than the true value. The mean is the best estimator of population size, and, provided that a decision can be made as to the distribution appropriate to the data, standard errors may be appended to it.

It appears that no one function, unless very general, will be capable of describing the observed distributions of animals in nature. Cole's theory has some merit as an approach to a general solution but must necessarily be modified to take account of contagion due to environmental heterogeneity and sociality. Since the aggregations due to these agents will vary with factors such as time of year, the appropriate function must also vary.

It is also certain that the efficiency of censusing and the distributions realized by these counting techniques depend on a thorough knowledge of the effect of environmental factors on the aggregation of animals. Reference to Allee's work (particularly Allee 1930) on animal aggregations shows few data but very little quantitative work.

Summary

1. Selected census distributions of two invertebrate species, *Cionella lubrica*—a snail, and *Trachelipus rathkei*—a sowbug, are given and characterized by the environmental factors at the time of census.

2. These distributions, and numerous others not here given, are fitted with 4 functions, the negative binomial, Neyman A, Polya, and, in some cases, the Cole.

3. It is shown that the Neyman A does not describe the distribution of either of the above animals.

4. The negative binomial and Polya distributions differed significantly from the observed distributions of *C. lubrica* in a few instances, and in most cases showed a definite lack of agreement with certain elements of the frequency distributions. It is therefore concluded that these functions are not suitable to describe the observed distributions of *C. lubrica*.

5. The same 2 functions show a constant discrepancy between observed and calculated elements of the distribution of *T. rathkei*, particularly where pairs and reproductive groups produced modes. It is concluded that these functions do not describe the distribution of this species.

References

Allee, W. C. 1931. Animal Aggregations. Chicago, University of Chicago Press.

Anscombe, F. J. 1948. The transformation of Poisson, binomial and negative binomial data. Biometrika **35**: 246-254.

———. 1949. The statistical analysis of insect counts based on the negative binomial distribution. Biometrics **5**: 165-173.

———. 1950. Sampling theory of the negative binomial and logarithmic series distribution. Biometrika **37**: 358-382.

Barnes, H., and **S. M. Marshall.** 1951. On the variability of replicate plankton samples and some applications of "Contagious" series to the statistical distribution of catches over a restricted period. J. Marine Biol. Assoc. U.K. **30**: 233-263.

Beall, G. 1935. Study of arthropod populations by the method of sweeping. Ecology **16**: 216-225.

———. 1940. The fit and significance of contagious distributions when applied to observations on larval insects. Ecology **21**: 460-474.

———, and **R. H. Rescia.** 1953. A generalization of Neyman's contagious distributions. Biometrics **9**: 354-386.

———, *et al.* 1954. Statistics and Mathematics in Biology. Ames, Iowa State College Press.

Bliss, C. I. 1953. Fitting the negative binomial distribution to biological data. Biometrics **9**: 176-200.

Bowen, M. F. 1947. Population distribution of the leafhopper in relation to experimental field plot layout. Jour. Agric. Res. **75**: 259-278.

Cole, L. C. 1946a. A study of the cryptozoa of an Illinois woodland. Ecol. Mon. **16**: 49-86.

———. 1946b. A theory for analyzing contagiously distributed populations. Ecology **27**: 329-341.

Evans, D. A. 1953. Experimental evidence concerning contagious distributions in ecology. Biometrika **40**: 186-211.

Feller, W. 1950. An Introduction to Probability Theory and Its Applications. New York, John Wiley and Sons.

———. 1953. On a general class of contagious distributions. Ann. Math. Stat. **14**: 389-400.

Fisher, R. A. 1950. Statistical Methods for Research Workers. New York, Hafner Publishing Co.

———. 1953. Note on the efficient fitting of the negative binomial. Biometrics **9**: 197-200.

———, and **F. Yates.** 1949. Statistical Tables for Biological, Agricultural, and Medical Research. New York, Hafner Publishing Co.

Greenwood, M., and **G. U. Yule.** 1920. An inquiry into the nature of frequency distributions representative of multiple happenings, etc. J, Roy. Stat. Soc. **83**: 285-295.

Jackson, C. H. N. 1939. Analysis of an animal population. Jour. Anim. Ecol. **8**: 238-246.

Jensen, P., C. R. Mapes, and **J. H. Whitock.** 1955. Pasture management and control of the lancet fluke (*Dicrocelium dendriticum,* Rudolphi, 1819). The Cornell Vet. **35**: 526-538.

Li, C. C. 1948. An introduction to Population Genetics. Peiping, China, National Peking University Press.

Mapes, C. R. 1951. Studies on the Biology of *Dicrocoelium dendriticum* (Rudolphi, 1819) Looss, 1899 (Trematoda; Dicrocoeliidae), including its relation to the intermediate host, *Cionella lubrica* (Müller). Cornell Vet. **31**: 382-432.

Marshall, J. 1936. The distribution and sampling of insect populations in the field with special reference to the American bollworm, *Heliothus obsoleta,* Fabre. Ann. Applied Biol. **23**: 133-152.

McGuire, J. V., T. A. Brindley, and **T. Bancroft.** 1957. The distribution of European corn borer larvae, *Pyrauste nubilalis* (Hbn) in field corn. Biometrics **13**: 65-78.

National Bureau of Standards. Applied Mathematics Series 14: 1951. Table of Exponential Functions.

———. P. W. A. 1941. Table of Natural Logarithms III.

Neyman, J. 1939. On a new class of contagious distributions applicable in entomology and bacteriology. Ann. Math. Stat. **10**: 35-57.

Pilsbry, H. A. 1948. Land Molluscs of North America (North of Mexico). Phila. Acad. Nat. Sci.

Poisson, S. D. 1837. Recherches sur la probabilité des jugements en matières criminelles. Paris.

Polya, G. 1931. Sur quelques points de la théorie des probabilités. Ann. de l'institute Henri Poincaré **1**: 117-162.

Skellam, J. G. 1952. Studies in statistical ecology. Biometrika **39**: 346-362.

"Student." 1907. On the error of counting with a haemocytometer. Biometrika **5**: 351-355.

———. 1919. An explanation of deviations from Poisson's law in practice. Biometrika **12**: 211-215.

Whitaker, L. 1914. On the Poisson law of small numbers. Biometrika **10**: 36-71.

Wright, S. 1935. Sizes of population and breeding structure in relation to evolution. Science **7**: 430-431.

AN EXPERIMENTAL ANALYSIS OF DISPERSAL IN THE FLOUR BEETLE, *TRIBOLIUM CONFUSUM*

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INTRODUCTION

Very few statements that can be made in biology have absolute generality. One of the few is the following: The three processes effecting the growth of any population in space and time are natality, mortality and dispersal (Allee *et al.* 1949, p. 272, paraphrased). Natality and mortality have been studied in a great variety of organisms from a great variety of points of view in both the field and the laboratory. Dispersal, or more precisely the spatial distribution of organisms, has been studied for many species but almost exclusively in the field.

Two criticisms can be raised against most field studies. First, conditions usually are not controlled; second, the effects of natality, mortality and dispersal are often confounded.

This paper is concerned with an analysis of dispersal as exhibited by the flour beetle *Tribolium confusum* when maintained in the laboratory. The point of view is ecological, but, for the present, dispersal is considered as a behavioral process distinct from natality and mortality. The choice of *T. confusum* was made on grounds of personal familiarity, convenience—and most importantly—the suitability of the species for populational experiments (Park, 1934). The experiments to be described were designed so far as possible to fulfill the assumptions of randomness involved in quadrat sampling.

Rather than burden this short introduction with generalities, hypotheses and literature review are relegated to the discussion section after the experiments have been presented.

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Materials and Methods

Husbandry

Rearing of *Tribolium confusum* is easy (Park 1934, 1937). Eggs were collected from stock jars and about 2000 were placed in a rearing jar containing 75 grams of medium (95% bran-free whole wheat flour and 5% brewer's yeast). This was set into an incubator controlled at 29°C and 70% relative humidity. When sexes were to be distinguished, which was usual, pupae were collected after about 25 days, segregated according to sex (Park 1934), and returned to the incubator to eclose at standard conditions. After eclosion, and at least 2 weeks before use in each experiment, the sexes were mixed, but the mutant ebony for black body (Park *et al.* 1945) was employed to distinguish the sexes. Ebony animals had been reared in the same jars with the wild-type animals. None were ever used experimentally until at least 40 days after eclosion.

Apparatus

Three types of apparatus were used; they will be referred to as the 48-vial General Environment (48GE), the 10-chamber General Environment (10GE) and the 10-vial Preferendum Apparatus.[2]

Except for the number of vials and methods of construction, which are apparent in Figure 1, the 48GE and 10GE devices are identical. The Preferendum Apparatus differs from the other two by having a bolting cloth screen that divides each chamber to form a cage at the bottom in which animals can be entrapped. Since the upper surfaces of the three types of apparatus are very similar, most of the remarks in the rest of this section apply to all.

The surfaces, illustrated in the photographs (Figures 2 & 3), consisted of round flour-filled holes opening flush on rough but unpatterned drawing paper, and forming a ring which was enclosed by a metal cover.

The geometrical features of the apparatus are important in the experiments. The arrangement of essentially identical vials on a ring puts each into the same relations with the peripheral barrier and other vials. The total area is admittedly small. Still, some surface must be traversed in passing from chamber to chamber, and the greatest part of the whole environment is barren. The small size has the advantage that large temperature and humidity gradients should not exist over short distances. Finally, a logical place to introduce beetles into the environment is provided, namely in the middle of the paper surface.

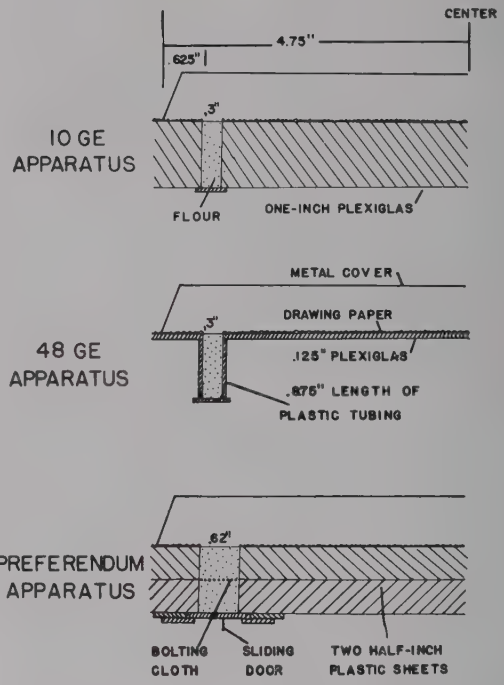

FIG. 1. Diagrammatic cross-sections of the three types of apparatus.

Experimental Procedures

Vials were filled with medium and the apparatus was dropped twice from a height of 5 centimeters; one centimeter mounds of medium were laid over each vial and the apparatus was dropped twice again. Before all excess medium was finally removed, its pattern was inspected for non-uniformities.

Animals were poured on the middle of the paper surface and the metal cover was set into place. The set-up was shelved on a turntable in an incubator controlled near 29°C and 70% R.H.; incubator air was forced to circulate vertically. From time to time turntables, which were sus-

ance and for criticisms which forced clear proofs. Debt is due to Drs. Jerzy Neyman and Elizabeth L. Scott for mathematical advice and encouragement. I am also indebted to the following for assistance in various ways: Dr. William Kruskal, Dr. Sewall Wright, Dr. Dennis Strawbridge, Dr. Herman Slatis, Dr. Earl R. Rich, Mr. Frank Sonleitner, Dr. Monte Lloyd, Mr. Arthur Ghent, Mr. James Bond, Catherine Naylor, and an anonymous editorial referee.

[2] In referring to the apparatus, the words "vial" and "chamber" will be used synonymously; the term "niche unit" will appear in the general discussion section. A niche unit will be one of the definite sites or masses of material which in the collective and abstract constitute a niche or habitat niche.

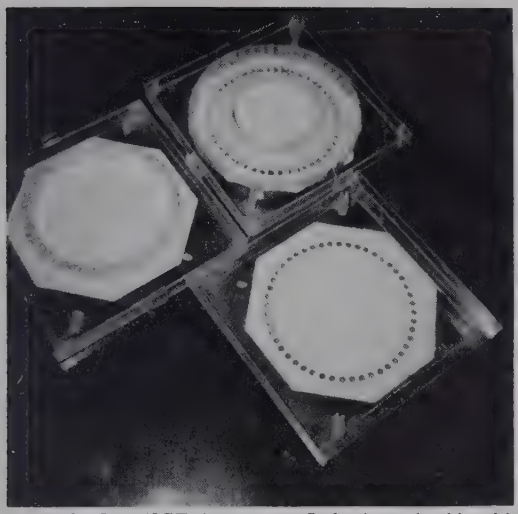

FIG. 2. The 48GE Apparatus. Left, the underside with 48 plastic vials; upper center, top surface with radially partitioned corral in place; right; upper surface with faint circle to mark position of metal cover.

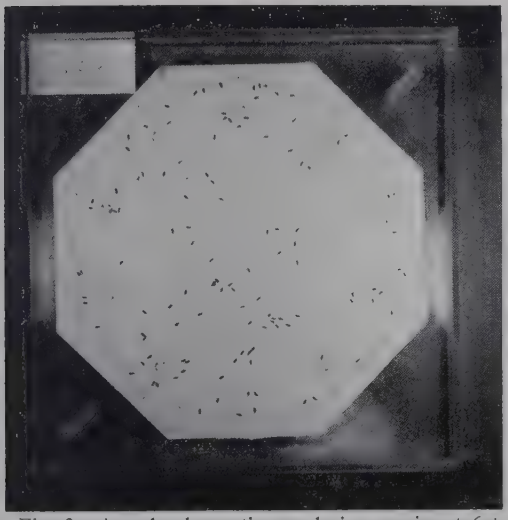

Fig. 3. A male observation made in experiment 6 to show the upper surface of the 70GE apparatus and the general appearance of an apparatus in actual use. The metal cover, which lay on the pencilled circle, was taken away a fraction of a second before the photograph was made.

pended one above the other, were advanced through quarter turns.

After a waiting period (46 hours in the first experiment, but usually 22 hours) one apparatus was gently removed from the incubator. The metal cover was promptly taken off and all beetles on the surface were brushed to the middle with a filing card. A stiff cork ring was then set over the openings to the vials. Animals on the surface were suctioned up into a shell vial. A radially partitioned corral replaced the cork ring, and beetles clinging to the underside of the ring were added to those taken from the surface. The corral isolated the openings of the chambers from one another; any beetle leaving a vial was now confined to the surface near that particular vial. The contents of each chamber were then suctioned at leisure into individual shell vials. The 49 or 11 vials were set aside and vial-by-vial counts of the animals were later made as the beetles were sifted out of the medium. When the same animals were used to reconstitute a similar experiment, all were reintroduced into the apparatus at the center.

Experimental Results

The experiments fall into 2 sections. The first section (experiments 1, 2 and 3) consists of quadrat studies; these descriptive experiments show that *Tribolium confusum* adults distribute themselves non-randomly over equivalent niche units and their patterns of distribution give evidence of interactions among the animals. The second section (experiments 4, 5 and 6) consists of analytic studies designed to assess the mechanism by which the animals interact to produce deviations from randomness. Of the 2 groups of experiments the quadrat studies are technically simpler but statistically more complicated. Before presenting the results, an orientation concerning the statistical methodology of the first section seems advisable.

Statistical Orientation

Consider a sample of N unit areas containing T organisms and for simplicity assume that the mean number of organisms per unit ($\bar{x} = T/N$) is an integer. At one extreme, if the distribution of organisms were perfectly uniform every area would contain exactly $\bar{x}$ organisms. In the intermediate case, the numbers of organisms in different unit areas could vary somewhat. At the other extreme, the distribution could be so variable that one unit contained all T organisms while the other N-1 were empty.

If, for the population from which the sample was drawn, the equivalent unit areas were very numerous and a very large number of organisms were dispersed independently, the conditions for a Poisson distribution would be approximated and a pattern of intermediate variability would be expected.[3] The mean, $\bar{x}$, and the variance, s^2,

[3] It can be shown that the total number of organisms and areas is irrelevant if information is incomplete and restricted to the sample, because the conditional distributions for a Poisson series and the actual multinomial are identical.

should be approximately the same and the ratio $s^2/\bar{x}$ should be near unity. Fisher (1950) has shown that if the population of counts is Poisson the Index of Dispersion (ID) which is equal to $(N-1)s^2/\bar{x}$ has a chi-square distribution with N-1 degrees of freedom. If the counts are perfectly uniform ID = 0. With intermediate variability ID is approximately equal N-1. When the variability is great ID takes on a large value, the maximum occurring when all the organisms are in one place. The Index of Dispersion thus is a quantification of dispersal pattern. Significance of the deviation of ID from its expected values of N-1 can be tested by reference to a chi-square distribution. When the number of degrees of freedom, df, is large, $t = \sqrt{2\chi^2} - \sqrt{2df - 1}$ has a normal distribution with mean zero and variance one. Negative values of t are symptomatic of uniform patterns; positive values of t indicate contagiousness or patchiness.

The tests of significance based on the Index of Dispersion have these immediate biological interpretations.

1. Uniform distributions of the organisms—ID too small or t negative—indicate that the organisms repel each other.
2. Variable distributions—ID too large or t positive—mean either that the organisms are gregarious and attract each other or that all parts of the environment are not equally attractive to the organisms.
3. "Random" distributions—ID near N-1 or t near zero—may represent a balance between conditions which simultaneously tend to both uniform and variable distributions.

These interpretations remain unchanged if the Indices from several samples are simply added and the total tested against the chi-square distribution with degrees of freedom equal to the sum of those for the several samples.

Statistical summaries contain two correlation coefficients. The coefficient for animals in adjacent units ($r_{xx'}$) was derived in a conversation with Drs. Jerzy Neyman and Elizabeth L. Scott of the University of California (Berkeley). Let the units have circular order and let x be the number of animals in any unit and x' the number in the next unit. Make all pairings of xx', that is x_1x_2, x_2x_3, x_3x_4, . . . , x_Nx_1. The correlation between numbers in adjacent units can then be computed as:

$$r_{xx'} = \frac{N\Sigma xx' - (\Sigma x)^2}{N\Sigma x^2 - (\Sigma x)^2}$$

This statistic should be sensitive to the effects of possible gradients and asymmetrical packing of the medium.

An editorial referee has astutely pointed out that the mean value of $r_{xx'}$ is $-1/(N-1)$, and not zero, when no correlation exists. Furthermore, although the statistic can be formally computed when N is 2 or 3, it is meaningless unless N is 4 or more. Even approximate tests of significance are laborious (see appendix note); it will be used not too rigorously, therefore, in this paper.

When the sexes are distinguished the correlation between sexes within chambers, r_{MF}, can be computed by the well-known formula.

Experiment 1

Distributions among 48 Vials under Four Densities of Introduction; Sex Ignored

Eight groups of wild-type animals were randomly selected without regard to sex, as below:

Beetles in Group	Number of Groups
1,200	2
800	2
400	2
100	2

Two sets containing a group of each size were constituted. These sets were alternately introduced into the four 48GE devices. Vials were censused at 2-day intervals. Ten observations on each were programmed; one 1200 observation was discarded when seepage from a humidity pan occurred.

The statistics of the observations, 79 in all, are presented in Table I. In each column the upper 10 values are in the order in which they were obtained from a group of animals. The next 4 lines are a statistical summary for the group. The next 14 lines give corresponding information for the alternate group of the same size. The overall statistical summary, which is obtained from the complete columns, contains all items of major interest as summarized in the following paragraphs:

(1) With decreasing introduced numbers (left to right), the values of t increase from a low negative to a high positive value. The two-tailed probabilities associated with the t's are significant for all introduced numbers except 400. The mean Index of Dispersion which should be 47 is approximated only in the 400 column. When 1200 animals are in the 48GE apparatus, the ones in the flour are distributed very uniformly; 800 achieve significant uniformity; 400 apparently distribute themselves randomly; and 100 animals are

TABLE I. Mean numbers of animals per niche ($\bar{x}$), Indices of Dispersion, 47 d.f. (ID), and Correlations between Adjacent niches ($r_{xx'}$) of Observations on the Distributions of Eight groups of animals at four introduction densities and ten independent introductions per group; waiting time two days

	1200			800			400			100		
Time Order	$\bar{x}$	ID	$r_{xx'}$	$\bar{x}$	ID	$r_{xx'}$	$\bar{x}$	ID	$r_{xx'}$	$\bar{x}$	ID	$r_{xx'}$
1	9.88	48.9	.350	7.15	27.1	−.026	3.92	48.9	.270	1.67	82.0	−.185
3	7.67	41.6	.190	6.57	39.5	.133	3.65	38.7	.213	1.00	56.0	.107
5	8.48	56.8	−.110	6.19	84.9	.522	3.67	40.5	.112	1.33	78.5	.044
7	6.83	33.2	−.028	5.40	37.0	−.173	3.02	41.4	−.072	1.31	76.4	.043
9	6.13	39.4	−.210	5.27	54.5	.127	3.42	23.9	−.224	.96	56.0	−.243
11	5.94	55.4	−.016	4.79	35.5	−.018	2.83	42.6	−.177	.90	47.4	.011
13	9.54	24.7	.237	7.25	30.5	.186	4.31	42.7	.240	1.29	54.1	.128
15	8.79	34.1	−.017	6.58	30.7	.200	3.94	38.9	−.058	1.35	44.4	−.038
17	8.71	40.9	.101	6.67	42.4	.052	4.00	53.0	.108	1.17	41.7	−.007
19	9.63	32.8	−.155	6.10	34.5	−.174	4.67	50.3	−.001	1.48	87.9	.215
Means	8.16	40.8	.034	6.20	41.7	.087	3.74	42.1	.041	1.25	62.4	.008
Sums	—	408	—	—	417	—	—	421	—	—	624	—
t	—	−2.10			−1.75	—	—	−1.63	—	—	4.70	—
P		.036			.080			.103			.0000	
2	7.06	37.8	.082	5.83	41.6	.378	3.29	53.4	.125	1.42	42.1	.061
4	—	Lost	—	4.60	37.2	.067	2.25	48.4	−.018	1.31	81.0	.003
6	7.15	48.1	.067	5.83	46.4	.002	2.56	55.3	−.255	1.19	51.6	.005
8	6.46	34.4	.085	4.58	24.4	.203	3.33	69.8	.037	1.23	57.8	.106
10	6.40	31.5	−.013	5.94	53.4	.006	3.88	34.9	−.087	1.40	68.4	−.016
12	8.40	29.7	−.262	6.06	39.1	−.098	3.85	40.5	−.074	1.35	104.1	−.007
14	8.85	26.7	.034	6.35	42.2	−.272	3.50	58.1	−.037	1.44	39.1	.279
16	7.98	35.2	−.171	5.77	41.7	−.127	3.69	45.6	.374	1.31	70.3	.144
18	9.98	43.0	.128	7.31	58.6	−.016	4.17	57.8	−.014	1.46	90.5	.060
20	10.65	38.2	.101	7.21	34.9	.059	3.88	35.9	.131	1.58	49.1	−.069
Means	8.10	36.1	.009	5.95	41.9	.020	3.44	50.0	.018	1.37	65.4	.057
Sums		325			419			500			654	
t		−3.61			−1.68			.97			5.52	
P		.0003			.092			.332			.00000	
OVERALL												
Means	8.13	38.54	.022	6.07	41.8	.053	3.59	46.0	.030	1.31	63.9	.032
Sums		733			836			921			1278	
t		−3.99			−2.44			.44			7.22	
P		.0001			.015			.660			.00000	

aggregated in the vials. The trend is one that might be explained by saying that at low densities the animals either aggregate or respond to minor differences in the environment, while—as density increases—"population pressure" overcomes the influences producing aggregation and in fact forces uniform patterns of distribution.

(2) Since some of the animals are always outside the vials an interesting trend in the proportion which actually enter the flour is rather obvious. If each mean is multiplied by 48 over the introduced number the series .33, .36, .43 and .63 is obtained. Thus as the number of animals introduced into the apparatus decreases, proportionately more are found in the flour.

(3) All the mean values of $r_{xx'}$ are small. The referee, however, points out that if it is assumed that the expected median is equal to the expected mean, — 0.021, there is an excess of coefficients above the assumed median, when Table I is considered as a whole. This very conservative argument leads to the conclusion that because of the extensive sampling a small correlation between adjacent units has been detected. Positive correlation, however, is symptomatic of environmental heterogeneity which cannot be the explanation for the low Indices of Dispersion in the 1200 and 800 groups. In the 100 group the highest ID is associated with a negligible $r_{xx'}$, as is the second highest; the third highest ID is associated with a substantial positive coefficient, but the fourth has a low negative coefficient. The lowest ID, which happens to be well below 47, is the one with the highest of all coefficients in the column. On the whole, it seems safe to say that technical variability had an unimportant effect.

The statistics of alternate pairs of test groups are satisfactorily consistent and there is no trend that need be attributed to the aging of the beetles. However, there is a noticeable tendency for mean densities of all groups which were in the incubator at the same time to rise and fall together. The lowest means in any column occurred in the eleventh observational period (sixth line down).

The first and twentieth periods were high. The synchrony of the mean densities is imperfect but would have to be taken into account and would complicate a rigorous analysis of the proportions entering the flour. The synchrony does not seem operative outside the columns of mean densities.

Experiment 2

Distributions of 400 Animals When the Sex-ratio Varies

In experiment 1 sex of beetles was ignored. In the present experiment sex-ratio is varied while density is held constant at 400 *Tribolium* per environment. The objective of this experiment is to examine further the trends seen in the first experiment.

Six groups, each containing 400 animals, were established as follows:

Group	Sex and Mutants
1	200 wild-type males, 200 ebony females
2	200 ebony males, 200 wild-type females
3	400 wild-type males
4	400 ebony males
5	400 wild-type females
6	400 ebony females

Six observations were made on groups 1 and 2; three on each of the others.

Table IIA shows the raw statistics for the mixed-sex groups 1 and 2 in an arrangement which corresponds as closely as possible to that in Table I. Each observation now produces 3 sets of statistics—one set for the males, one for the females, and one for all animals when sex is ignored (total). The correlation between the sexes (r_{MF}) is arbitrarily entered on the "Total" line.

TABLE IIA. Mixed-sex data from Experiment 2. Mutant Ebony was used reciprocally to distinguish the 200 males from 200 females. "Total" statistics are obtained when sex is ignored as in Table I, 400 column

Mutant & Sex	Time Order	$\bar{x}$	I.D.	$r_{xx'}$	r_{mf}
w. m.		0.979	47.98	.042	
e. f.	1	2.646	37.41	.121	
Total		3.625	54.41	.042	0.376
w. m.		0.438	49.86	−.146	
e. f.	2	2.354	31.00	.027	
Total		2.792	46.53	−.070	0.440
w. m.		1.104	114.55	.486	
e. f.	3	2.729	32.79	−.151	
Total		3.833	54.43	.248	−0.034
w. m.		0.813	63.15	.006	
e. f.	4	2.625	36.29	.051	
Total		3.438	52.89	−.007	0.252
w. m.		1.000	88.00	−.125	
e. f.	5	2.271	33.24	.099	
Total		3.271	55.48	.261	0.110
w. m.		1.500	50.67	−.053	
e. f.	6	2.771	26.88	.033	
Total		4.271	38.75	−.106	0.010
e. m.		1.417	68.94	.221	
w. f.	1	2.542	34.59	−.149	
Total		3.958	58.59	.146	0.250
e. m.		1.250	92.00	−.043	
w. f.	2	2.708	36.89	.049	
Total		3.958	51.01	−.010	−0.061
e. m.		1.021	53.86	.054	
w. f.	3	1.813	32.72	−.062	
Total		2.833	38.35	.135	−0.049
e. m.		1.604	43.31	.093	
w. f.	4	2.479	29.03	−.028	
Total		4.083	25.88	.006	−0.253
e. m.		1.583	45.26	.121	
w. f.	5	1.813	37.14	−.099	
Total		3.396	47.55	−.208	0.162
e. m.		1.708	51.46	.079	
w. f.	6	2.063	28.52	.014	
Total		3.771	34.07	−.074	− .127

TABLE IIB. Mean statistics and analysis of indices of dispersion of mixed-sex data

Group Means	$\bar{x}$	ID	$r_{xx'}$	r_{MF}	Total ID	t	Prob. of t
Wild males	.972	69.04	.035		414	5.06	.0000
Ebony females	2.566	32.94	.030		198	−3.87	.0001
Total	3.538	50.42	.061	.192	303	.87	.38
Ebony males	1.431	59.14	.088		355	2.91	.001
Wild females	2.236	33.15	−.046		199	−3.79	.0001
Total	3.667	42.58	−.001	−.013	255	−1.12	.26
All males	1.201	64.09	.062		769	5.65	.0000
All females	2.401	33.05	−.008		396	−5.41	.0000
All totals	3.603	46.50	.030	.090	558	.17	.43

The summaries of mean statistics and tests of significance are displayed separately in Table IIB, the last line of which deserves attention first. Here the 12 new observations have produced the same means of $\bar{x}$, ID and $r_{xx'}$ as the 20 original observations in Table I.

Throughout Table II, however, there is evidence that the two sexes have quite different dispersal behavior. With convincing consistency, the mean density of males is lower than the density of females. (On a 50-50 chance basis such a set of 12 comparisons has a two-tailed probability of $(\frac{1}{2})^{11}$, or about .0005.)

With equally convincing consistency, the male Indices of Dispersion exceed those for the females. Furthermore, the summed male ID, as judged by the high positive values of t, shows significant aggregation; the female ID, judged by the low

negative values of t, shows significant uniformity or a tendency for the females to repel one another.

Intrasexual interactions are strong but intersexual interactions evidenced in r_{MF} are weak.

The question to consider now is whether the sexes retain their characteristic distributions when they are apart. Table III shows that they do. For a two-tailed test by chi-square the 5% critical values of the Index of Dispersion would be 30.0 and 67.8. Since 3 of the 6 male ID's are significantly high and 4 of the 6 female ID's are too low, the tests of the summed ID's are almost superfluous. For each group the probability is .0000.

TABLE III. Single-sex observations from Experiment 2

Time Order	Mutant and sex	$\bar{x}$	ID	$r_{xx'}$
1	Wild male	0.79	78.2	−.034
3	" "	1.13	61.7	.047
5	" "	3.03	129.0	.024
4	Ebony male	3.54	89.2	−.073
6	" "	5.73	64.5	−.283
7	" "	5.88	67.6	−.055
	All-male means	3.35	81.7	−.062
	Sum		490.1	
	t		7.58	
	P		.0000	
2	Wild female	3.81	18.2	.149
4	" "	2.83	32.0	−.001
6	" "	2.92	28.7	−.183
1	Ebony female	3.71	28.6	−.029
3	" "	4.38	26.8	.062
5	" "	4.92	31.3	−.041
	All-female means	3.76	27.6	−.007
	Sum		165.5	
	t		−5.54	
	P		.0000	

Experiment 3

Studies in the 48GE Apparatus on Mixed-Sex Groups of 800 and 200 Animals; Ebony Is Sex Marker

The clear difference in dispersal behavior between the 2 sexes raises the question of how this difference might operate in mixed-sex groups to produce over-all apparent aggregation in fewer than 400 animals and overall uniformity in more than 400. In an attempt to throw some light on this question, mixed sex groups of 200 and 800 animals (with ebony used as a sex marker as in experiment 2) were set up for 6 observations each in the 48GE apparatus.

The results are disappointing in terms of their comparison with the findings of experiment 1. The average statistics on the "All Totals" lines in Table IVB are more like those previously observed for groups of 400 and 100 animals rather than the ones that were anticipated for the groups of 800 and 200 that were actually used. The poor reproducibility encountered in this experiment makes it necessary to consider the following comments as tentative.

TABLE IVA. Raw statistics from Experiment 3. Groups containing a total of 800 or 200 animals were studied in the 48GE apparatus. Sex-ratio was 50:50, ebony mutant being used to distinguish the sexes

Mutant & Sex	Time Order	800 $\bar{x}$	800 I.D.	800 $r_{xx'}$	800 r_{MF}	200 $\bar{x}$	200 I.D.	200 $r_{xx'}$	200 r_{MF}
w. m.	1	1.58	52.8	.068		0.71	47.9	−.150	
e. f.		1.88	27.3	−.073		0.81	33.6	−.062	
Total		3.46	45.1	.051	.160	1.52	52.6	−.100	.308
w. m.		1.88	104.1	.257		0.77	70.7	−.046	
e. f.	2	2.85	29.4	.154		0.75	25.3	.368	
Total		4.73	79.8	.311	.384	1.52	60.5	.228	.288
w. m.		1.73	72.6	−.124		0.67	64.0	.086	
e. f.	3	2.46	28.4	.156		1.00	36.0	−.167	
Total		4.19	43.8	−.080	−.065	1.67	56.8	.081	.204
w. m.		1.31	52.0	.028		0.52	76.8	−.026	
e. f.	4	2.40	31.5	.059		0 96	29.1	−.110	
Total		3.71	44.7	−.013	.154	1.48	51.4	−.106	.121
w. m.		0.85	60.9	−.020		0.42	66.4	−.024	
e. f.	5	1.69	31.0	.178		0.83	34.4	.093	
Total		2.54	40.9	−.020	−.004	1.25	69.6	.069	.544
w. m.		1.17	112.0	−.224		0.65	69.6	−.067	
e. f.	6	1.75	26.9	−.128		0.85	23.4	−.001	
Total		2.92	64.3	−.327	.064	1.50	50.7	−.053	.184
e. m.		1.96	63.3	.015		0.63	62.8	−.070	
w. f.	1	3.01	25.6	.114		1.27	35.8	−.033	
Total		5.00	32.4	−.068	−.203	1.90	49.8	.026	.115
e. m.		2.06	58.6	−.117		0.92	45.5	.400	
w. f.	2	2.79	50.1	−.079		0.96	37.5	−.058	
Total		4.85	47.4	−.061	−.118	1.88	46.5	.163	.125
e. m.		1.96	55.1	.120		1.00	106.0	−.113	
w. f.	3	2.98	35.2	.228		1.15	26.2	.133	
Total		4.94	43.5	−.038	.009	2.15	68.0	.020	.089
e. m		1.56	84.4	−.206		0.42	61.6	−.052	
w. f.	4	2.21	29.8	−.047		0.90	27.3	−.062	
Total		3.77	43.0	−.083	−.189	1.31	47.5	−.075	.243
e. m.		1.44	77.8	.070		0.60	65.3	−.039	
w. f.	5	2.21	41.6	.216		0.56	42.3	−.050	
Total		3.65	57.3	.311	.026	1.17	60.6	−.132	.120
e. m.		1.40	69.8	.220		0.54	55.2	.164	
w. f.	6	1.85	35.6	−.091		0.90	25.1	−.112	
Total		3.25	45.8	−.101	−.090	1.44	31.9	.040	−.127

Considering that males aggregate and females repel each other, one can offer 4 hypotheses for the change from apparent over-all aggregation at low densities to apparent uniformity at high densities.

(1) If the males contributed a higher proportion to the over-all $\bar{x}$ at lower densities their ag-

TABLE IVB. Mean Statistics and Analyses of I. D.

	$\bar{x}$	ID	$r_{xx'}$	r_{MF}	Total ID	t	Prob. of t
800 ANIMALS							
Wild males	1.42	75.7	−.002		454	6.42	.0000
Ebony females	2.17	29.1	.058		175	−5.04	.0000
Total	3.59	53.1	−.013	.116	319	1.52	.13
Ebony males	1.73	68.2	.017		409	4.87	.0000
Wild females	2.51	36.3	.057		218	−2.85	.004
Total	4.24	44.9	−.007	−.094	270	−0.51	.60
All males	1.57	71.9	.007		863	7.98	.0000
All females	2.34	32.7	.057		393	−5.55	.0000
All totals	3.92	49.0	−.010	.011	588	0.73	.47
200 ANIMALS							
Wild males	0.62	65.9	−.038		395	4.39	.0000
Ebony females	0.87	30.3	.020		182	−4.66	.0000
Total	1.49	56.9	.020	.275	342	2.41	.02
Ebony males	0.68	66.1	.048		396	4.43	.0000
Wild females	0.95	32.4	−.030		194	−4.02	.0000
Total	1.64	50.7	.007	.094	304	0.94	.35
All males	0.65	66.0	.005		792	6.22	.0000
All females	0.91	31.3	−.005		376	−6.15	.0000
All totals	1.56	53.8	.013	.185	646	2.37	.02

gregation would more than balance the lack of variability in females. However, since for the 800-group the "all males" $\bar{x}$ is .40 of the "all totals" $\bar{x}$, and for the 200-group the figure is .39, the first explanation is not supported.

(2) Male aggregation might increase at lower density. But the reverse, if anything, is true.

(3) Female distribution may be more uniform at higher density. But the reverse, if anything, is true.

(4) Correlation between the sexes may be higher at the low density. This is a distinct possibility. For the 800-groups the average r_{MF} is .011 and 6 of the 12 values contributing to this average have negative signs; in other words, correlation is near zero. But for the 200-groups r_{MF} has a mean of .185 and 11 of the 12 values have positive signs. The two-tailed probability of 11 of the same signs out of 12 coefficients in .006. This, the fourth hypothesis, finds further elaboration in the discussion section.

Experiment 4

Responses of the Two Sexes to "Conditioned" Medium

The first of the analytic series of experiments is designed to open the question of the types of behavioral mechanisms that are necessary to account for the interactions evident so far. The particular point considered is whether behavior is mediated by changes in the flour occupied by beetles.

Prolonged occupancy of flour by *Tribolium confusum* populations produces "conditioning" which involves energy depletion, biochemical change and physical change (Park and Woollcott 1937). The conditioned medium used in this experiment had been inhabited by a reproducing laboratory stock for about 3 months. "Fresh flour" is self-explanatory. Both media were allowed to stand in an incubator at 29°C, 70% R.H. for at least 2 weeks.

For each observation 5 chambers in a 10GE apparatus were filled with conditioned medium and another 5 were filled with fresh flour. Eighty ebony males and 80 wild-type females were introduced and censused as usual after one day. In reporting the results (Table V) only the totals for 5 chambers containing conditioned or fresh flour are given.

TABLE V. Data from Experiment 4. Preferences of test animals for vials containing conditioned or fresh medium

Observation Number	MALES IN NICHES		FEMALES IN NICHES	
	Conditioned	Fresh	Conditioned	Fresh
1	42	12	34	20
2	37	21	37	19
3	38	16	35	20
4	36	12	27	17
Pooled Totals	153	61	133	76
P	.00000		<.002	

The probabilities given are those of observing as great or greater differences in the pooled totals if they were drawn from a binomial population with p of 1/2. Similar results were obtained with medium that had supported about 10 imagoes per gram for 2 weeks.

It seems rather clear that both sexes of *Tribolium confusum* choose conditioned medium. The astonishing observation that the beetles select almost completely depleted food rather than wholly unused food deserves more elaborate analysis. Arthur Ghent, using methods more suitable for such analysis, had already made the same observation in the Chicago laboratory of Thomas Park. The experiment here merely shows that Ghent's independent but prior results obtain under circumstances relevant to the study of dispersal.

The preference of the males for conditioned medium would be consistent with the supposition that their tendency to aggregate is mediated by changes animals have imposed on the flour. The same preference of the females, however, cannot be part of the mechanism leading to uniform distributions; differences in conditioning would introduce environmental variability thereby produc-

ing too large, rather than too small, values of the Index of Dispersion.

Experiment 5

Choices of Chambers in the Preferendum Apparatus when the Subcompartments Contain Males or Females or Are Empty

The results of experiments 2 and 3 indicate that there may be strong intrasexual interactions. Females act as if they are repelled by the presence of other females; their interactions definitely seem to take place within the flour. Males, on the other hand, are perhaps attracted to each other in the flour and/or react very strongly to environmental irregularities not necessarily dependent on the presence of other animals.

To demonstrate that the animals can actually react to the presence of other animals in the flour, the following experiment was performed. Three preferendum apparatuses were constructed for simultaneous use. As usual, the observation period was one day. In one apparatus the subcompartments below the coarse bolting cloth in 5 chambers contained 50 entrapped males per chamber, while the alternate 5 contained only fresh flour; in another apparatus 5 cages each contained 50 trapped females and the other 5 fresh flour; in the third apparatus the chambers contained trapped males and females, alternately.

The animals used were all wild-type. In the mixed-sex observations one sex was marked by a small spot of aluminum paint on an elytron; the single-sex group opposite to that one in sex was also marked. After every 3 periods the 200 males of the single-sex group were combined with the 200-female group and the 400 beetles of the mixed-sex group were segregated by sex. The paint marks did not affect behavior in any apparent manner.

The results given in Table VI are pooled totals for four observations. Probabilities are as defined in experiment 4. The findings may be summarized as follows. When the choice was between chambers with trapped beetles of either sex and those with just flour, males in single-sex groups entered chambers with trapped animals; when all the chambers contained trapped beetles and the choice was between male and female chambers, males in the single-sex groups chose female chambers. In mixed-sex groups—no matter how the subcompartments had been filled—males showed no preference at all. On the other hand, females (of both types of test groups) selected non-occupied chambers rather than those with trapped animals, when exposed to these choices. If all the subcompartments contained animals, the females showed a greater toleration for males.

TABLE VI. Tests in preferendum apparatus. 50 males (M), 50 females (F) or no animals (—) in each subcompartment. Figures given are pooled totals for four observations, at each of which 200 animals of each sex present were introduced

Test Animals	M	—	P	F	—	P	M	F	P
Males Alone	79	36	.0001	91	30	.0000	30	52	.02
Females Alone	47	151	.0000	51	187	.0000	132	103	.06
Mixed-sex									
Males	43	58	.15	46	66	.05	28	44	.076
Females	49	143	.0000	49	194	.0000	120	81	.006

Thus it appears that *Tribolium* of both sexes have the capacity to detect and respond to the presence of beetles in flour. The pattern of interactions that emerges in this experiment is complex, but it will be restated and fully interpreted in the discussion section.

Experiment 6

The Relation between the Distributions of Animals on the Surface and within Chambers

In the time that the experimental animals spend on the barren paper surface they are possibly interacting with others there and are probably responding to uncontrolled environmental heterogeneities. The local biological and physical conditions may partly influence selection of holes to enter. The following experiment was undertaken originally to assess both influences, but unfortunately produced information only on the effects of environmental heterogeneity.

When groups of 160 animals were introduced into the 10GE apparatus, no new variables were involved but the distribution of beetles on the surface was photographed immediately after the metal cover was removed. Although mixed-sex groups were employed in this experiment they will not be reported. As in experiment 5, paint was used to distinguish the sexes, but the available camera did not resolve the paint marks (or a difference in color between ebony and wild-type).

In Table VII the means of densities and Indices of Dispersion have the same significance as in the early experiments. The statistic called "Surface Chi-square" is computed exactly as is ID, but the counts of the animals are taken from the 10 sectors of surface around chambers in a photograph.

The 10GE apparatus is similar to the 48GE apparatus except that the distance between holes is about 16 times as great. Therefore it is important to note that, despite the increased distance, females within chambers are distributed too uniformly and males are aggregated. Other studies

TABLE VII. Data from Experiment 6. The probabilities shown are each for one tail of the Chi-square distribution for 36 degrees of freedom. The total female ID is tested as too small a value; the total male ID and each total Surface Chi-square is tested as too large a value

$\bar{x}$	ID	Surface Chi-square
Male Observations		
7.20	22.2	10.4
9.00	18.0	15.6
4.10	3.6	11.3
6.40	37.3	10.8
Total	81.1	48.1
P	.0000	.09
Female Observations		
7.60	3.7	16.6
8.90	4.8	7.2
8.60	4.0	7.0
8.40	3.9	23.2
Total	16.4	54.0
P	.03	.03

of a pilot nature to test the comparability of 10GE to 48GE observations confirm these results.

Since high values of Surface Chi-square would result from pronounced gradients, it is very satisfying to note that females, rather than males, by virtue of their somewhat irregular distributions on the surface, are the ones to be suspected of sensitivity to physical non-uniformities. It thus seems reasonable to take the position that interactions within the flour, not poor technique, explain the patterns of behavior of the two sexes.

Discussion

The Specific Results

If sex is ignored the spatial distribution of a population of *Tribolium confusum* imagoes depends on density. Superficially there seems to be a response to "population pressure" in the sense that a tendency to aggregate at low densities gradually gives way to a very marked uniform distribution at high densities.

Within the imago population the 2 sexes differ in their behavior. Males spend less time in the flour than females and are attracted by animals of either sex, preferring females slightly. Females spend a good deal of the time in the flour and are repelled by animals of either sex, although they tolerate males more than other females.

The "population pressure" effect observed in mixed-sex populations seems to depend entirely on the correlation between the sexes. The results of experiment 5 provide a basis for explaining how correlation between the sexes could change with density while the strengths of intrasexual interactions apparently remain constant.

At low densities, even if the females distribute themselves rather uniformly, there will be some sites without females. Positive correlation will result when males respond to the qualitative distinction between chambers without females and ones with a few. As density increases this distinction will tend to disappear and so will intersexual correlation. The diminution of the latter may be reinforced by the females' weak negative response to males; this response, in turn, will introduce variability into female distributions which compensates partially for increased uniformity attributable to female-to-female interactions. An inverse but similar type of reasoning applies to male distributions.

Under the explanation just given intrasexual interaction would tend to appear independent of density in mixed-sex populations such as those studied in experiment 3. However, experiment 2 provides exidence that these interactions really increase with density. The 400 males of the single-sex groups produced much higher ID's than the 200 males of the mixed-sex groups; correspondingly, the 400 females had somewhat lower ID's than the 200 females.

In experiment 5 the free animals obviously could be reacting only to an olfactory stimulus penetrating the porous bolting cloth screen from the trapped animals. Such a mechanism is bound to be density-dependent.

Experiment 4 (with conditioned flour) demonstrates that the interactions, at least among the females cannot be explained in terms of mediation of the environment. The olfactory mechanism provides an explanation of the behaviors of both sexes in terms of immediate interactions. However, the possibility of aggressive contacts has not been excluded and study of this aspect is indicated.

Therefore it would be desirable to evaluate the importance of the olfactory mechanism in populations of *Tribolium confusum*. It seems to be very great. Roth (1943) found specialized glands in the abdomen and prothorax of *T. confusum;* obviously homologous glands occur in related tenebrionid beetles and perhaps other arthropods. The specific products of these glands were identified in *Tribolium castaneum* as quinones; ethylquinones and toluiquinones were shown to repel *T. castaneum* imagoes (Loconti and Roth 1953) and the suggestion was made that the glands may be a defense against predators. This may well be a function of the glands, but it is probably less important than the effect on dispersal of the adults.

In *T. castaneum* both sexes were repelled by the glandular products; the effect on *T. confusum* is not known.

With conditioning flour becomes energy-poor and granular. Since Loschiavo (1952) found that *T. confusum* preferred energy-rich and fine medium, it is hoped that forthcoming studies by Ghent will clarify an apparent discrepancy between Loschiavo's observations and results in experiment 4.

Generalization of the Results to a Model of Population Behavior

The experiments reported here are behavioral, but the intention from their inception was that they, and future studies, would be conducted in the context of population ecology. The purpose of this section is partially to supply that context.

Like the majority of insect (or even animal) species, *Tribolium confusum* is vagile, asocial, sexual, highly fecund, relatively shortlived, herbivorous, small and cryptozoic.

This list of commonplaces can be interpreted so as to emphasize behavioral and spatial relevancies. Vagility is the ability to make active place-to-place movements. Asociality implies that individuals can survive and reproduce outside of structured groups of proximate animals. Highly fecund females, once inseminated, may be independent of males for long periods of time. The rough rule may be stated that herbivorous adults and their progeny find both food and shelter in a niche with fixed location in space. Short-lived animals must respond quickly to environmental cues; learning and other cumulative processes are probably of secondary importance. The cues will impinge constantly on all the senses of small cryptozoa.

From the foregoing remarks and from the results of the experiments with *Tribolium confusum*, these 4 points seem to follow:

(1) For feeding and egg laying, gravid females will tend to select niche units of low occupancy or avoid those of very high occupancy.

(2) Well-fed animals will spontaneously leave any niche unit.

(3) Gravid females will generally spend time in niche units according to an inverse relationship to occupancy.

(4) Males may not obey rules (1) and (3) but must be attracted to the general neighborhood of females.

Rule (2) would insure that some tendency for the species to disperse would persist even when "population pressure" is negligible. Rule (4) makes allowance for the possibility that males of a particular species may be important genetically but not ecologically. The other two rules lay stress on the responses of females to "niche occupants"; the latter is intended as a term which may simply mean other females but may refer also to males or progeny.

In the experiments on *T. confusum* a very simple population, consisting only of imagoes, was studied. The innate rules of behavior that the individuals followed were exactly those that have been outlined in this section. The important thing to focus on, of course, is that the females entered vials in order to feed and oviposit. When the apparatuses were censused practically no eggs were found on the barren paper surface while enormous numbers of eggs were sifted out of the flour. In distributing themselves so uniformly, the females effectively distributed what would have been the next generation if the environment had not been disturbed. The survival value to the species is obvious; few suitable sites would be "overlooked" and few would be so crowded by the hatching larvae that their chances of surviving to adulthood would be impaired.

In a newly opened habitat or at the beginning of a breeding season a species may be often represented by a population consisting entirely of adults. However, progeny will eventually appear or may already be present. It would be of advantage to the species if the gravid females responded to levels of "occupancy" by developing progeny. If they did so according to the 4 axioms of behavior, the following adjustments in dispersal would take place automatically:

(1) A female will be more likely to deposit more than one egg in a niche unit when the density of progeny is low.

(2) When density is high the females will spend proportionately less time laying eggs and competing for food with the already hatched young stages.

(3) Since females spend more time outside niche units at high densities, even random movements will increase the chance that they will enter unexploited regions.

(4) Whether the distribution of progeny is aggregated or random at low densities, because of the responses of females the distribution will become more uniform at high densities.

From the point of view of population genetics the scheme that has been just outlined has some drawbacks since inbreeding may be promoted at low densities. On the whole, however, such a system of dispersal behavior would seem to contribute to the survival of the population and of the species.

Discussion of the Literature in Terms of the Generalization

Less work has been done relevant to the previous section than may be thought. Although field quadrat studies are numerous, variability introduced from various sources (Beall 1939, Salt and Hollick 1946) precludes assessment of more subtle interactions. Evidence similar to that obtained in experiments 4, 5 and 6 must be available so that reasonable interpretations can be made.

It is likely that simple suppositions about the value of low initial density of progeny may have to be qualified. Ghent (1955) showed that not only do individual female sawflies lay clusters of eggs on jack-pine needles, but the presence of a cluster increases the probability that another female will lay her cluster contiguously. The explanation seems to be that first instar larvae must cooperate in attacking the tough needles; intense competition and mortality eventually reduce initial aggregations.

Situations which seem to fit the scheme previously sketched are known. In *Drosophila melanogaster,* Chiang and Hodson (1950) found that larvae "interfere" with oviposition, which therefore is dependent on the density of progeny. In the chalcid parasitoid *Trichogramma evanescens,* Salt (1937) found that larvae will inhibit oviposition if the females fail to respond to the scent of other females' tracks on the host eggs.

It would be surprising to find for any species that dispersal alone regulated density or that behavioral considerations were important only in dispersal. Mortality of immature stages has already been shown to be density-dependent because of cannibalistic behavior in *Tribolium confusum* (Rich 1956). Understanding of the growth process in this species is emerging because the varied studies on it (Neyman, Park and Scott 1956) have been both populational and experimental.

Summary

The behavior of *Tribolium confusum* imagoes was studied as they distributed themselves among discontinuously located, but equally accessible, vials of flour, under controlled laboratory conditions.

1. If sex is ignored, imagoes aggregate in the vials at low overall density; apparently distribution themselves randomly at intermediate density; and distribute uniformly at high density.

2. As density increases proportionately fewer imagoes enter the flour.

3. Females spend more time in flour than do males.

4. At all densities, and in mixed-sex or single-sex groups, females distribute themselves uniformly and males aggregate.

5. The qualities of male and female distributions in mixed-sex populations are seemingly unaffected by increasing density; the change in the quality of the distribution of mixed groups apparently depends solely on decrease of correlation between the sexes with density.

6. Physical gradients and cumulative effects of beetles' activities were not the main determinants of the observed dispersal patterns. Interactions in the flour within and between the sexes are shown to depend on olfactory stimulus, presumably from glands which the species is known to have. The scent of other beetles, especially females, repels females. Males are attracted by the scent of others, especially females.

7. The behavior of the animals is interpreted as an adaptation which enables populations of the flour beetle to adjust spatial distributions so as to promote survival of the species.

Appendix Note

Dr. Jerzy Neyman in a letter supplies the formula for the variance of $r_{xx'}$. The squared standard error, SE^2, of the correlation between numbers on a circle is

$$\frac{N^2 - 3N + 3}{(N-1)^2(N-2)} - \frac{N}{(N-1)(N-2)} \cdot \frac{\Sigma(x_i - \bar{x})^4}{[\Sigma(x_i - \bar{x})^2]^2}$$

The significance of an observed correlation, say r, can be approximately tested when N is large by taking

$$\frac{r + (1/N-1)}{SE}$$

to be a unit normal deviate. Note that SE is the square root of the variance. Since the fourth power of deviations from the mean is involved, the computation of the more than one hundred variances was deemed utterly impractical for the present studies.

References

Allee, W. C., A. E. Emerson, O. Park, T. Park, and **K. P. Schmidt.** 1949. Principles of Animal Ecology. Philadelphia, Saunders.

Beall, G. 1939. Methods of Estimating Populations of Insects in a Field. Biometrika **30**: 422-439.

Chiang, H. C., and **A. C. Hodson.** 1950. An Analytical Study of Population Growth in *Drosophila melanogaster.* Ecol. Monogr. **20**: 173-206.

Fisher, R. A. 1950. Statistical Methods for Research Workers. 11th ed. New York, Hafner.

Ghent, A. W. 1955. Oviposition Behavior of the Jack-pine Sawfly, *Neodiprion americanus,* as Indicated by an Analysis of Egg Clusters. Can. Ent. **87**: 229-238.

Loconti, J. D., and **Louis M. Roth.** 1953. Composition of the Odorous Secretion of *Tribolium castaneum.* Ann. Ent. Soc. Amer. **46**: 281-289.

Loschiavo, S. R. 1952. A Study of Some Food Preferences of *Tribolium confusum.* Cereal Chem. **29**: 91-107.

Neyman, J., T. Park, and **Elizabeth L. Scott.** 1956. Struggle for Existence—the Tribolium Model: Biological and Statistical Aspects, in J. Neyman, ed., Proceedings of the Third Berkeley Symposium on Mathematical Statistics and Probability. vol. IV, pp. 41-79. Berkeley, University of California.

Park, T. 1934. Observations on the General Biology of the Flour Beetle, *Tribolium confusum.* Quart. Rev. Biol. **9**: 36-54.

———. 1937. The Culture of *Tribolium confusum.* in J. G. Needham, ed., Culture Methods for Invertebrate Animals. Comstock.

———, **B. Ginsburg,** and **Shirley Horwitz.** 1945. Ebony: a Gene Affecting the Body Color and Fecundity of *Tribolium confusum.* Physiol. Zool. **18**: 35-52.

———, and **Nancy Woollcott.** 1937. Studies in Population Physiology VII: The Relation of Environmental Conditioning to the Decline of *Tribolium confusum* Populations. Physiol. Zool. **10**: 197-211.

Rich, E. R. 1956. Egg Cannibalism and Fecundity in *Tribolium.* Ecology **37**: 109-120.

Roth, L. M. 1943. Studies on the Gaseous Secretion of *Tribolium confusum* II. The Odoriferous Glands. Ann. Ent. Soc. Amer. **36**: 397-424.

Salt, G. 1937. The Sense Used by *Trichogramma* to Distinguish between Parasitized and Unparasitized Hosts. Proc. Roy. Soc. B **122**: 57-75.

———, and **F. S. Hollick.** 1946. Studies of Wireworm Populations II. Spatial Distribution. J. Exp. Biol. **23**: 1-46.

FLOW, TEMPERATURE, SOLAR RADIATION, AND ICE IN RELATION TO ACTIVITIES OF FISHES IN SAGEHEN CREEK, CALIFORNIA

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As pointed out by Hubbs and Trautman (1935), Maciolek and Needham (1952), and Benson (1953), a study of winter conditions in streams is a badly neglected phase of freshwater ecology. Most stream surveys and studies are conducted in summer when weather is hospitable. However, a fundamental characteristic of high mountain trout waters is the possession of a relatively short, pleasant summer season while, over the rest of the year, generally severe conditions prevail with low temperatures, floods, ice, and snow.

It is well known that severe winter conditions cause extremely high mortalities of trout, as indicated by the work of Needham and Slater (1945), Needham, Moffett and Slater (1945), Maciolek and Needham (1952), Nielson *et al.* (1957), and Miller (1958). Tack (1938) reports that ice crystals plugged the mouths and gills of trout in ponds and killed them by suffocation. Reimer's (1957) work indicates that such heavy winter mortalities are due more to adverse and exhaustive physical conditions than to food conditions at this season. Despite these observations, the factors that actually cause heavy mortalities of stream-dwelling animals remain to be clearly defined and measured. It is the purpose of this paper to present the effects of certain of these physical factors on stream conditions and on the activities and well-being of fishes during winter periods. These studies were conducted at the Sagehen Creek Project operated under the University of California. This project is located at an elevation of 6,337 feet on the east slope of the Sierra Nevadas in the Tahoe National Forest, 12.8 miles north of Truckee, California.

Sagehen Creek is a tributary of the Little Truckee River which flows into the main Truckee River near the California-Nevada state line. Averaging around 15 feet in width, it is fed by springs and melting snow and fluctuates from around 50 cubic feet per second during spring run-off to about 2.0 c.f.s. in September. It rises at an elevation of around 7,000 feet and after passing over its 10 mile course, enters the Little Truckee at an elevation of 5,000 feet. The winter studies described here were all conducted within a half mile of the station headquarters. The facilities provided there have been described by Needham (1956).

Sagehen Creek basin is entirely forested except for scattered meadows along the stream. The dominant trees consist of Jeffrey pine (*Pinus Jeffreyi*), white fir (*Abies concolor*), red fir (*Abies magnifica*), and lodgepole pine (*Pinus contorta*) which dominates the wetter areas. The average winter snow pack is roughly 44 inches. Severe winter conditions usually prevail from mid-December to the end of March with intermittent periods of clear weather occurring for short intervals.

The only native salmonid fish in Sagehen Creek was the Lahontan cutthroat trout, *Salmo clarki henshawi,* but these have long since been replaced by introduced forms: eastern brook trout, *Salvelinus fontinalis;* rainbow trout, *Salmo gairdneri;* and brown trout, *Salmo trutta.* These 3 species all occur in the area of the station and the only

other species of fish that is present in this area is the sculpin *Cottus beldingi*.

Of the salmonids, rainbow trout are most abundant, followed by eastern brook, with brown trout being relatively scarce. The last is the dominant species, however, in the beaver ponds on the lower portions of the stream.

Facilities and Methods

In order to make outdoor observations for fairly long periods of time in cold weather, one of the first essentials is shelter for the observer. At Sagehen Creek this was provided in an underwater observation tank. This was fitted with four, 15 × 23 inch plate glass windows, two to a side, for viewing the hydrohabitat below the stream surface (Needham 1956).

A series of thermocouple stations was established around the tank in various positions for recording both air and water temperatures. Air temperature was measured in the shade of the roof eve on the north side of the tank about 12 feet above the water. Surface-water temperatures were measured from one inch to about 16 inches below the water surface. No differences were found in these measurements because of the turbulence of the stream in this area. Ground-water temperatures were measured at the downstream end of the tank where a relatively large volume of water upwelled from the gravel stream bottom beneath the tank.

One station set up on the stream bank to measure solar radiation, used a Gier and Dunkle flat-plate radiometer. Because of difficulties encountered in making an underwater solarimeter watertight, no measurements were made of the penetration of solar radiation through water. The copper-constantan thermocouples were attached to a selector switch and an ice bath standard inside the tank. A lead-covered cable was run from this some 400 feet to the laboratory where it was connected to a Leeds and Northrup No. 8662 potentiometer. Thus, two workers were required: one in the tank to select the stations where temperatures were being taken, and the other in the laboratory to record the readings on the potentiometer. Telephones connected the tank with the laboratory.

The observer in the tank, aside from selecting the stations for temperature measurements, also made observations on the behavior of any fishes seen. In subzero weather this was a rigorous task to say the least, and during the 24-hour diurnal studies reported here, this job was rotated between two or more workers. Students quickly dubbed this work "the deepfreeze." The bottom of the tank was floored with wood. On this, Air Force litter blankets and air mattresses were placed to reduce the hardship. Even though heavily clothed, an observer could not usually stand more than about 45 minutes lying in the tank before he would have to return to the station headquarters to warm up.

Lights were provided for night observations. Strong white light invariably disturbed or drove away fish in areas adjacent to the tank windows but subdued red or violet light modified their behavior only slightly. However, any light that was strong enough to permit the observer to see clearly, usually frightened or drove fishes away. The use of infra-red light was considered but abandoned because of its rapid absorption in water.

A second series of thermocouple stations was set up at a location 500 yards downstream from the tank site. This location will be referred to subsequently as the truck-crossing site.

Water levels were measured with a Leopold-Stevens water-stage recorder (type A35), installed about 200 yards below the truck crossing. A rating curve established for this station permits conversion of gage heights into discharge in cubic feet per second.

Air and water temperatures at the station headquarters were taken constantly with a two-pen recording Bristol thermograph, using 12-inch charts and operated the year round. The bulb recording air temperatures has a 10 foot lead and is mounted on the north side of a tree about 3 feet above the instrument in a small cupola to protect it from direct rays of the sun. The water lead is 50 feet long and is buried in the ground from the tree into the stream. There the bulb is placed in an iron pipe in swift water about 3 feet from the bank and at a depth of about one foot at normal flows.

Results

Seasonal Characteristics of Air and Water Temperatures

Sagehen Creek is characterized by a marked seasonal variation in temperature. Temperature records show that the most stable period, temperature-wise, is in winter and that the least stable period is in summer. Water temperatures, obviously, are strongly influenced by air temperatures. Daily thermograph charts show that air and water temperature curves have similar shapes but the latter show a smaller range between maximum and minimum temperatures and the temperature fluctuations lag several hours behind those of the air.

The greatest differences between mean monthly maximum and minimum water temperatures occur in July and August. In the former month the difference was 21.5°F and in the latter, 14.4°F (Figure 1). The smallest differences occurred in December and January and were 6.2°F and 4.3°F respectively. These small winter differences may be accounted for, in part at least, by the much smaller amounts of solar energy reaching the stream and its environment in the winter than in the summer. Also, during the winter much heat may be stored as latent heat of fusion during ice formation without further lowering of the water temperature.

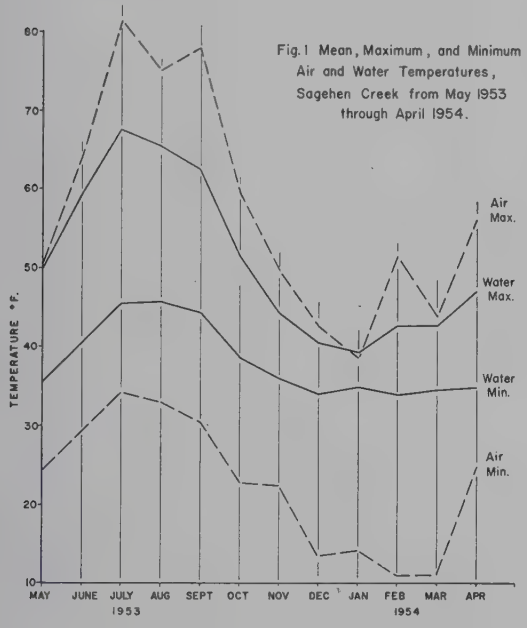

Fig. 1 Mean, Maximum, and Minimum Air and Water Temperatures, Sagehen Creek from May 1953 through April 1954.

In terms of actual, daily minimum water temperatures, 32°F was first recorded on October 26, 1953, when the air temperature dropped to 18°F. In November, 32°F was recorded on 4 days; December 6 days; January 2 days; February 5 days; and March 3 days. Daily minimum water temperatures never dropped to 32°F during the months of April through September.

The maximum daily water temperature recorded during the period covered was 70°F on August 11, 1953. The mean maximum for this month was 65.2°F. In July a maximum of 69.0°F was recorded on 8 days while the mean maximum for this month was 67.3°F or 2.1°F warmer than the mean for August.

In Fig. 1, it is of interest to note that mean monthly minimum air temperatures of less than 32°F occurred in 10 months of the year (September through June). Individual daily minima below 32°F are encountered each month of the year. In July, 1953, the air temperature dropped to 32°F or below on 15 days. Similarly, August produced 18 days below 32°F.

Acclimation

The observed water temperature pattern is one of gradually decreasing temperatures in October and November with the reverse occuring in April, May and June. In relation to survival of fishes, these observations clearly indicate that 2 long periods of temperature acclimation are provided, one in fall and one in spring. The former gradually prepares fish for adjustment to the low water temperatures of December through March and the latter to the high temperatures of June through September.

Trout are relatively stenothermal animals but the temperatures recorded for Sagehen Creek are all well below the maximum tolerance limit of 78°F reported for eastern brook trout by Embody (1921) and Fry *et al.* (1946).

The senior author observed a kill, estimated at 50%, when 15,000 3 to 4 inch rainbow trout were planted in Convict Lake in eastern California. The water temperature of the lake was 45°F whereas the fish had been reared for approximately 6 months in a hatchery at a water temperature of 63°F. From this and other observations, it is concluded that acclimation must be a continuous and necessary process under natural conditions, one that is essential for the continual readjustment to changing thermal conditions from month to month and season to season. Lack of a thorough acclimation process may provide one answer at least to the extremely heavy losses of hatchery-reared trout following planting as reported by Needham (1949), Miller (1958), and other workers.

Diurnal Cycles in Air and Water Temperatures and Solar Radiation

Twenty-four hour temperature and solar radiation patterns were measured for 4 different periods of the year. Three of these were taken in clear weather in February, August, and October. Only one was taken in stormy weather in January. These periods were selected because they provide data typical of the behavior of these factors in relation to seasons and weather conditions. Clear weather usually prevails during summer periods while intermittent storms may occur at other seasons of the year. All of these observations were made manually without the use of a constant recorder.

The amount of solar energy reaching the stream shows a characteristic pattern for each season. On January 15-16, 1954 (Figure 2), the weather was stormy and maximum solar radiation reached only 31 BTU/hr/ft.^{2} The air temperature over the same period fluctuated only between 28.4°F and 14.8°F. Water temperatures were between 32.0°F and 33.3°F. Surface-water temperatures remained slightly below those of the ground water throughout the period.

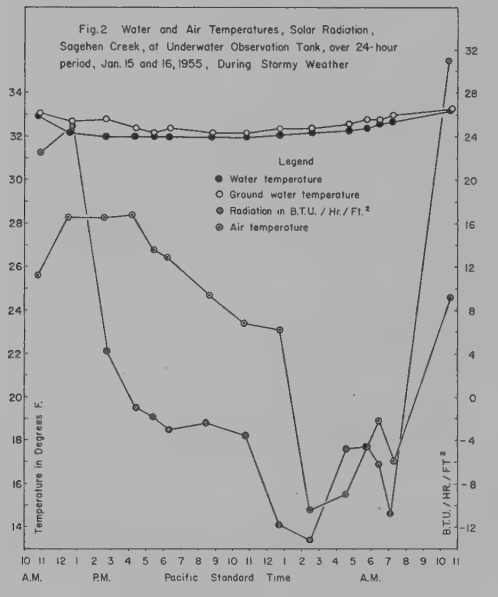
Fig. 2 Water and Air Temperatures, Solar Radiation, Sagehen Creek, at Underwater Observation Tank, over 24-hour period, Jan. 15 and 16, 1955, During Stormy Weather
Legend
Water temperature
Ground water temperature
Radiation in B.T.U. / Hr. / Ft.^{2}
Air temperature
Temperature in Degrees F.
B.T.U. / HR. / FT.^{2}
A.M. P.M. Pacific Standard Time A.M.

In contrast, periods of clear weather in winter produced larger fluctuations in radiation and temperature but the variations still are moderate compared to other seasons of the year. On February 3-4, 1954 (Figure 3), radiation reached a maximum of 147 BTU/hr/ft^2, and a minimum of —16 BTU/hr/ft^2. Air temperature varied between 52.3°F and 5.4°F. However, the water temperature varied only between 37.0°F and 32.0°F. The ground-water temperature again exerted a modifying influence on the temperature of the surface water. During the day, when air temperature was high, the surface-water temperature was higher than that of the ground water. However, from 6:15 PM to 10:30 AM the surface-water temperature fell to below that of the more stable ground-water temperature.

As indicated above, extremes in temperature fluctuations occur during the summer period as is shown on August 12-13, 1955 (Figure 4). Air temperatures varied from 77.2°F to 31.0°F. Solar radiation varied from 204 to —23 BTU/hr/ft^2.

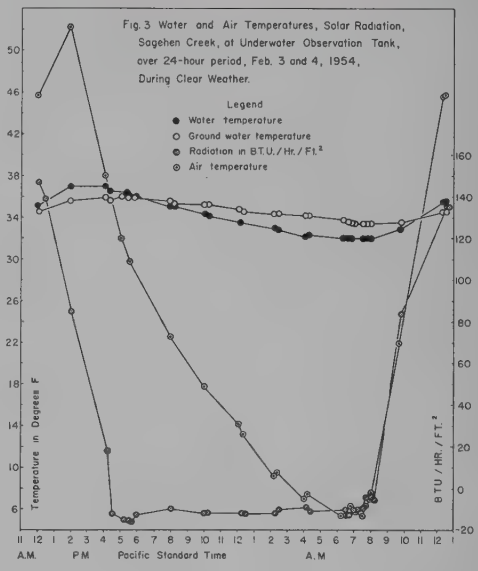
Fig. 3 Water and Air Temperatures, Solar Radiation, Sagehen Creek, at Underwater Observation Tank, over 24-hour period, Feb. 3 and 4, 1954, During Clear Weather.
Legend
Water temperature
Ground water temperature
Radiation in B.T.U. / Hr. / Ft.^{2}
Air temperature
Temperature in Degrees F
BTU / HR. / FT.^{2}
A.M. P.M. Pacific Standard Time A.M

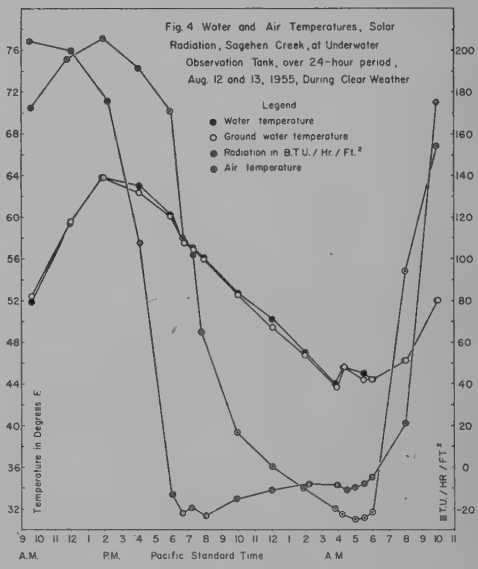
Fig. 4 Water and Air Temperatures, Solar Radiation, Sagehen Creek, at Underwater Observation Tank, over 24-hour period, Aug. 12 and 13, 1955, During Clear Weather
Legend
Water temperature
Ground water temperature
Radiation in B.T.U. / Hr. / Ft.^{2}
Air temperature
Temperature in Degrees F.
BTU / HR / FT.^{2}
A.M. P.M. Pacific Standard Time A.M

The temperatures of ground water and surface water were almost identical at all times and varied between 43.9°F and 63.8°F.

Conditions in autumn were intermediate between those of summer and winter. On October 28-29, 1954 (Figure 5), solar radiation varied from 100 to —10 BTU/hr/ft^2. Air temperature fluctuated between 58.9°F and 16.0°F. Water temperature varied between 41.0°F and 33.5°F.

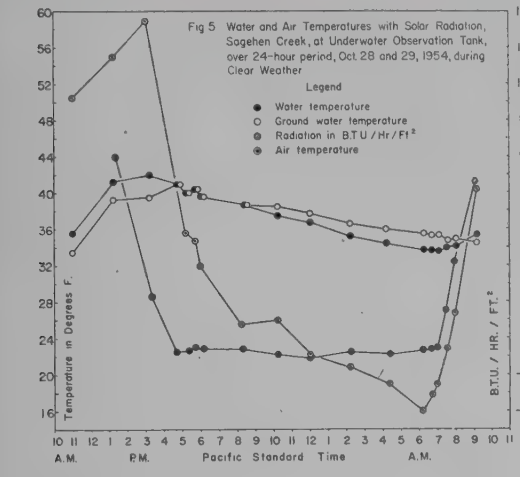
Fig 5 Water and Air Temperatures with Solar Radiation, Sagehen Creek, at Underwater Observation Tank, over 24-hour period, Oct 28 and 29, 1954, during Clear Weather
Legend
Water temperature
Ground water temperature
Radiation in B.T.U / Hr / Ft²
Air temperature
Temperature in Degrees F.
B.T.U. / HR. / FT.²
A.M.
P.M.
Pacific Standard Time
A.M.

The effect of ground water in exerting a modifying influence on the temperature of the surface water was again noticeable. During the day surface water was warmer than ground water but during the night it was cooler. Nightly reversal of the relationships between surface-water and ground-water temperatures during clear cold weather are clearly illustrated in Figures 3 and 5. When the radiation and air temperature fall rapidly in the late afternoon, the surface water slowly cools and usually drops below the temperature of the ground water between 7:00 and 9:00 PM. With the advent of daylight, increasing radiation and higher air temperatures cause the surface water to warm slowly, and its temperature rises above that of the ground water usually between 8:30 and 11:00 A.M. During stormy periods, as indicated above for January (Figure 2), the temperature of the surface water may consistently run below that of the ground water for full 24-hour periods.

It is evident from the above that both temperature and solar radiation show pronounced differences between summer and winter and between stormy and clear weather periods. The air temperature and radiation curves, in general, parallel each other. In summer, maximum radiation is usually reached between 9:00 and 10:00 AM Standard time, after which for the remainder of the day the amount of energy falls away sharply, becoming negative around 6:00 PM when more heat is being lost than is being gained. In winter, in both clear and stormy weather, solar radiation usually peaks between 12:00 noon and 1:00 P.M, after which it falls away rapidly and becomes negative between 4:00 and 5:00 PM.

Effect of Anchor Ice on Stream Flow

Anchor ice is a type of underwater ice that forms on the bottom of streams and on objects under water. In contrast, frazil ice particles are very small crystals and discs of underwater ice which are distributed throughout a turbulent flowing stream. Underwater ice forms only when the water temperature falls below 32.0°F. A temperature gradient from the ice to the water is required in order to carry away the latent heat of fusion. Thus, supercooling of the water and the rapid transfer of heat work together to cause the formation of underwater ice (Mantis 1951). Anchor ice is formed in riffles where it first appears as small white masses on the substrate. It is soft and mushy in consistency since it is a mixture of both liquid phase and ice particles. Key points of beginning formation are the upstream points of stones where the current is split to each side and where the current velocity is reduced nearly to zero. Although the reasons have not been definitely established, Dorsey (1948) suggests a purely mechanical action in which the motion of the water molecules is slowed sufficiently to enable them to orient themselves as required for crystallization. There is also an extension of growth by accumulation and adhesion of fine frazil-ice particles which are always found in supercooled water. In riffles the presence of turbulence and of irregular surfaces from which heat may be conducted away faster, often causes anchor ice to form to such an extent that it dams up the stream. At times anchor-ice dams will almost completely block all flow of water and will even extend some distance into pool bottoms above and below the riffles.

During the winter of 1953-54 the conditions under which anchor ice formed in Sagehen Creek and the effects of such formations were observed. Warm ground water seeping up from the substrate of the stream bed prevented the formation of anchor ice near the observation tank but it formed abundantly in the riffles at the truck-crossing site some 500 yards downstream.

The two observation sites differed considerably in their ecological settings. The truck crossing was fully exposed to the elements in an open meadow with the nearest trees some 50 feet away to the south. On the north the meadow extended about 200 feet to the lodgepole pines bounding the meadow's north border. The stream winds its way through the meadow with frequent pools and riffles and except for scattered willows and a few trees here and there, represents a typical high montane meadow.

The observation-tank site was located in what might best be called a semi-exposed habitat. A group of lodgepole pine growing on the south bank partially shades it and clumps of willow are far more numerous in the general area than at the truck crossing. The only meadow present is a narrow strip on the north bank some 50 feet wide in which the radiometer station was established. The upwelling of ground water at this site may be caused, partially at least, by the fact that the valley narrows materially at this point. About a hundred yards upstream the meadow widens again and the narrowing in between the upper and lower meadows could cause a damming effect in the substrate sufficient to create the upwelling observed.

Anchor ice usually formed at minimum night-time air temperatures of from — 9.0°F, the lowest reading of the period, to 12.0°F. However, on the morning of January 15, 1954, subsurface ice, similar to anchor ice, was observed in the stream, even though the minimum air temperature of the previous night was only 26.0°F. This may be explained by the presence of high winds during the night which blew snow into the stream, supercooled the water and resulted in a slushy snow and ice mixture which accumulated on the stream bottom.

During the course of the winter it was noticed that increasingly low temperatures were required to produce anchor ice. During the month of December anchor ice was observed on 11 out of the 15 mornings when the minimum air temperature was between 0.0°F and 12.0°F. However, in January, February and the first week of March, anchor ice was observed on only one out of the 25 mornings when the minimum temperature was in this same range. This is possibly due to an increased ice and snow cover over much of the stream, which would act as an insulator sufficient to prevent loss of heat and thus prevent underwater ice formation. Similar effects have been noted by Devik (1942, 1944) in preventing the formation of ice on underwater inlet gates. When minimum night-time temperatures were below 0.0°F, regardless of the month, anchor ice was observed each morning (a total of 7 times), with the exception of January 20 and 22, when the minimum temperatures were — 7.0°F and — 3.0°F, respectively.

As indicated above, anchor ice produces a marked effect upon stream water levels. In Figure 6, gage height and air temperature are graphed over a 72-hour period on December 28, 29, and 30, 1953, when suitable weather conditions for the formation of anchor ice prevailed. The dam formed by anchor ice in the riffle at the lower end of the gaging station pool caused the rise in levels depicted in the graph. From this it is apparent than an inverse relationship exists between temperature and water level. As the temperature drops, anchor-ice formation commences and the water level rises. Maximum and minimum water temperatures and the length of time the minimal period lasted, are given in Table I for the periods graphed in Fig. 6.

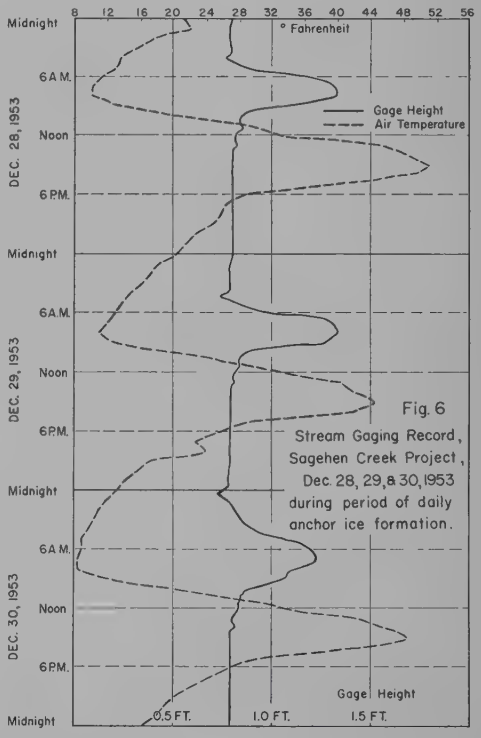

Fig. 6
Stream Gaging Record, Sagehen Creek Project, Dec. 28, 29, & 30, 1953 during period of daily anchor ice formation.

TABLE I. Water temperatures (°F.), December 28, 29, and 30, 1953, during period of daily anchor ice formation graphed in Figure 6

Date	Max.	Min.	Duration of Minimum
Dec. 28.....	40	32	5:30-8:30 A.M.
29.....	40	32	7:00-8:00 A.M.
30.....	39	32	2:00-8:00 A.M.

A thermocouple at the truck-crossing site was installed one inch above the water surface. With the rise in water level accompanying anchor-ice formation, this thermocouple was covered by water, thus providing information as to the time and temperature when anchor ice formed. For

example, on January 22-23, 1955, anchor ice formed between 4:15 and 6:00 AM at an air temperature of between — 3.0°F and — 4.0°F. The air temperature at the thermocouple just above the water surface was usually about 4°F above the air temperature recorded on the bank, probably influenced by its proximity to water. Once anchor ice formed around the thermocouple, the temperature varied between 29.4°F and 32.3°F. When the water temperature rose above 32.0°F, the anchor ice began to melt and pool levels dropped.

Water levels in the pools above the riffles where the dams form may be raised as much as 1.7 feet. However, the average maximum height of the water level for 20 nights when anchor ice formed was 1.31 feet. The water level height during the day was nearly constant at 0.81 feet. The rise began anywhere from 9:00 PM to 5:00 AM and lasted from a minimum of 2 hours to a maximum of 12 hours. The average duration was about 4 hours.

It will be noted in Figure 6 that the rise was preceded by a slight, sudden decrease in water level which varied from 0.01 to 0.05 feet and which lasted approximately one hour. This, we believe, represents the period when the water is supercooled and much of it is rather suddenly turned into ice, thus causing a slight lowering of stream discharge.

As soon at the damming effect of anchor ice becomes apparent, the water level begins to rise although the actual flow continues to decrease. Thus the increased gage heights shown in Figure 6 were caused by anchor ice and do not represent a real increase in stream discharge. Actual discharge on the dates these observations were made averaged 3.5 cubic feet per second.

Feeding of Trout in Winter

Trout were observed to feed on numerous occasions when the water temperature was between 32.0°F and 33.0°F. The fact that trout will actively feed when the water temperature is 32°F is clearly demonstrated by the following observation made in the large underwater observation tank on January 25, 1956. About a foot of fine snow had fallen during the previous night and about 7:00 AM a strong west wind started blowing large quantities of snow into the stream, both from the banks and from adjacent pine trees. The surface of the stream was practically occluded by floating clumps of snow. From the tank windows the undersurface of the floating snow was quite irregular and at several points clumps had been pushed against the stream bottom where the current was slack and unable to move it. That the water had been supercooled by the addition of snow blowing into it was apparent for the columns of snow touching the stream bottom appeared to grow and become larger by the addition of crystals of frazil ice during the observation period between 4:00 and 4:45 PM.

Three rainbow trout ranging from around 4 to 8 inches in length were observed actively feeding. Despite the fact that the water surface was completely covered by clumps of floating snow and that snow pressed against the bottom in places, these fish were actively swimming up to examine each food item drifting in the water. They would take particles in their mouths in a sort of "tasting" action and then either swallow or reject them. Occasionally fish were seen feeding directly off the bottom of the stream. They avoided the snow masses but ranged easily through the tunnel-like openings between the submerged snow masses. It is likely that the large masses of snow being swept downstream were dislodging aquatic insect larvae and nymphs from the stream substrate, thus offering a higher than normal quota of natural drift foods. Maciolek and Needham (1952) reported that the daily breakup of anchor ice caused it to rub over stones as it drifted downstream, thus freeing bottom food organisms which were rapidly consumed by trout.

This observation did not reaveal any cause of winter mortality except to the elements composing the macrofauna. The fish seemed vigorous and fed steadily during the 45 minutes they were under observation.

These winter feeding activities must reflect a rather high metabolic rate following acclimation to temperatures at or very close to 32°F. Fry (1947, p. 16) states that an "animal can exist, often for substantial periods of time, at a temperature level beyond the zone of tolerance and may frequently do so, particularly during diurnal fluctuations." This statement refers specifically to what Fry terms the "zone of resistance" to maximum temperatures following suitable acclimation. However, from the feeding observed we can only conclude that 32°F is still within the zone of tolerance for trout and that the zone of resistance, including the lower lethal limit for this species, must fall somewhat below the freezing point (Fry *et al.* 1946). While we have no precise measure of the magnitude of the activities observed, the main difference seemed to be one of speed. In feeding observed during summer periods, the actions of the fish were more rapid and their reactions in general seemed much faster.

Other Activities of Fishes

Trout observed during daylight hours were invariably seen in close proximity to shelter. This consisted of overhanging bushes, projecting snow banks, or a deep sheltered pool protected by exposed roots at the side of the underwater observation tank. This preference for cover or dark areas was reflected in the greater numbers of fish observed at night. During four 24-hour observation periods a total of 47 trout were seen at night while only 14 were seen during daylight hours. During the day trout probably moved away from the relatively shallow area surrounding the observation tank to deeper and darker areas of the stream. One 3½ inch eastern brook trout was observed intermittently for a period of 7 days close to the edge of the stream under an overhanging bank of ice and snow. This protected area was so dark even at midday that a spotlight was necessary to see the fish. At times during this period this same site was occupied by a 4½ inch eastern brook trout. However, at other times the position was vacant. During the same observation periods 25 sculpins were observed at night but only 7 during the day. However, the sculpins that were observed during the day were more likely to be found in unprotected, lighted areas of the stream than were the trout.

Territorial behavior of trout has been described by Newman (1956). Trout occupied particular sites in the stream and it was often possible to recognize an individual fish on the basis of its size, spotting, and location.

Interspecific aggressive behavior between sculpins and trout was observed. On one occasion a 4 inch sculpin gave chase to a 2 inch trout. The sculpin made a short dash in the direction of the trout but the trout quickly swam upstream out of reach. In 2 other instances, one involving a 4 inch sculpin and a 3½ inch eastern brook trout and the other a 3 inch sculpin and a 2½ inch eastern brook trout, the trout approached from upstream to within one inch of the sculpin and veered off slightly at it passed the sculpin which apparently was not disturbed.

At night trout maintained a closer relation to the substrate than during the day. Their lower fins were often in contact with the stream bottom and it is possible that tactile cues of position were substituted for visual ones.

Trout foods and other insect life were abundant and active during the winter. On a number of occasions in January, 1954, springtails (Collembola) were observed crawling on the surface of the ice covering stream pools and in the air spaces between layers of ice. In addition, mayfly and stonefly nymphs and simuliid and caddisfly larvae were seen regularly in small cavities between pebbles on the bottom of the stream. In the fall of 1955, a gravel spawning bed was constructed in shallow, swift water next to the downstream window on the south side of the tank. Sexually mature eastern brook trout of both sexes were penned inside the area with half inch mesh wire cloth. These fish proceeded to go through their courtship activities, dig their nests, and spawned within full view of the window. One redd was actually built in contact with the glass of the window and each step in the spawning process could easily be observed. Similar success in observing spawning of Atlantic salmon (*S. salar*) and Arctic charrs (*S. alpinus*) with observation chambers has been reported by Jones and King (1949) and Fabricius and Gustafson (1954).

Mortality of Fishes

Reflection on the problem of over-winter survival of fishes makes it appear that when heavy mortalities do occur as a result of severe winter conditions, they must happen quickly and in localized areas subject to sudden catastrophies. On the other hand, severe floods may cause heavy damage over entire drainage areas, the effects being greatest in the lower, wider portions of streams and least in their narrower headwaters.

Needham and Slater (1945) report the loss of several hundred trout when a snowbank dropped into a rearing pond at the Hot Creek State Fish Hatchery near Bishop, California. Nielson *et al.* (1957, p. 22) report parallel effects of snow and ice. Needham (1934, p. 243) reports a reduction from 205 to 70 pounds per acre of the macrofauna in Waddell Creek near Santa Cruz, California, which was probably a direct result of a heavy flood in early February, 1933.

A heavy flood occurred in Sagehen Creek in December, 1955. Flow in the creek peaked at *ca.* 700 c.f.s., the highest ever recorded for Sagehen Creek. The changes wrought in the stream bed were many and drastic. Numerous new channels were cut and stream bank erosion was severe. The pool on the north side of the observation tank was partially filled by gravel washed downstream. A loose rock dam just below the station was washed completely out, as were the 3 eastern brook spawning beds that held incubating eggs from spawning in the previous fall. Apparently the force of the flood had disastrous effects on fall-spawned eggs which were incubating in stream gravels for incoming young of eastern brook and brown trout of the zero age group were almost completely missing from the population samples taken the following summer.

Evidence of the disturbance and destruction of the elements of the macrofauna by anchor ice is reported by Benson (1955). His observations, made in the Pigeon River, Michigan, showed that square foot samples of anchor ice from the stream bed contained an average of 10 organisms plus sand, gravel, and organic debris. Floating anchor ice contained similar numbers of organisms and amounts of materials. Anchor ice served as a method for downstream dispersal of bottom organisms but the number moved was so small that it "would not be great enough to deplete the bottom fauna populations" (Benson, *op. cit.*, p. 530).

The causes of winter mortality of fishes dwelling in lentic waters at high elevations subject to severe floods and winter conditions may be listed as follows:

1. Sudden collapse of snow and ice into the water may cause death by either direct crushing effect or suffocation against the stream substrate, or both.
2. Both snow and anchor-ice dams and ice jams may dewater stretches of considerable length and suffocate fish life.
3. Suffocation may occur when flooded side channels or other areas are dewatered suddenly by the breakup and dispersal of ice and snow dams.
4. Severe floods may have the following effects, all of them severe and the cause of high mortalities of aquatic organisms:

(a) Actually killing both adults and young fishes by the grinding action of huge amounts of gravel being rolled down stream beds.

(b) Stranding of fishes in side pools that later dry up or that are easily accessible to predators.

(c) Destruction of a major portion of the macrofauna that forms the bulk of fish foods.

(d) Destruction of eggs and alevins of fishes through annihilation of spawning redds.

Summary

A study of ecological conditions in winter in relation to activity of fishes in Sagehen Creek, California, showed that there exist, temperature-wise, two long periods of acclimation, one in the fall and one in the spring. These prepare fish for both the low water temperatures of winter and the high temperatures of summer. Water temperatures show less fluctuation in winter than in summer both because of the smaller amount of net solar radiation and the storing of heat as latent heat of fusion during ice formation. Bottom macrofauna is abundant as food for trout in winter and trout were observed to feed on numerous occasions when the water temperature was between 32° and 33°F. It is concluded that 32°F is within the zone of tolerance of trout and that trout are able to resist water temperatures below 32°F for short periods of time. Floods may act as a decimating factor to fish populations by destroying eggs and reducing bottom macrofauna.

Anchor ice was shown to be an important ecological factor since it raises the water level in pools and reduces the flow over riffles. Anchor ice formed only in those areas of the stream which had no upwelling of relatively warm ground water through the substratum. Anchor ice, when it is breaking up, melting or otherwise dispersing, dislodges considerable amounts of the bottom macrofauna, thus making more food available to trout at such times.

Trout exhibited territorial behavior, showed a strong preference to occupy sheltered locations, and in shallow water were more numerous during the night than during the day.

The high winter mortalities of trout populations which have been observed are probably not the result of lack of food or long periods of low temperatures. More likely causes are sudden catastrophes such as severe floods or suffocation under collapsed snow banks or dewatering of stream sections by ice dams.

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References

Benson, N. G. 1953. The importance of ground water to trout populations in the Pigeon River, Michigan. Trans. N. Amer. Wildl. Conf. 1953, 269-280.

———. 1955. Observations on anchor ice in a Michigan trout stream. Ecology, **36**: 529-530.

Devik, O. 1942. Supercooling and ice formation in open waters. Geofys. Publ., **13**(8): 1-10.

———. 1944. Ice formation in lakes and rivers. Geogr. J., **103**(5): 193.

Dorsey, N. E. 1948. The freezing of supercooled water. Trans. Amer. Phil. Soc., **38** (Part 3): 247-328.

Embody, G. C. 1921. Concerning high water temperatures and trout. Trans. Amer. Fish. Soc., **51**: 58-61.

Fabricius, E. and **K. Gustafson.** 1954. Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. Institute of Fresh-water Research, Drottningholm, Rept. No. 35: 58-104.

Fry, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. 55, Publ. Ont. Fish. Res. Lab. 68.

———, **J. S. Hart,** and **K. F. Walker.** 1946. Lethal temperature relations for a sample of young speckled trout, *Salvelinus fontinalis.* Univ. Toronto Stud. Biol. 54, Publ. Ont. Fish. Res. Lab. 66.

Hubbs, C. L. and **M. B. Trautman.** 1935. The need for investigating fish conditions in winter. Trans. Amer. Fish. Soc., **65** (1935): 51-56.

Jones, J. W. and **G. M. King.** 1949. Experimental observations on the spawning behaviour of the Atlantic Salmon (*Salmo salar* Linn.). Proc. Zool. Soc., **119** (Part I): 33-48.

Maciolek, J. A. and **P. R. Needham.** 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. Trans. Amer. Fish. Soc., **81** (1951): 202-217.

Mantis, H. T., ed. 1951. Review of the properties of snow and ice. Eng. Expt. Station, Inst. of Technology, University of Minnesota, Minneapolis.

Miller, R. B. 1953. The role of competition in the mortality of hatchery trout. J. Fish. Res. Bd. Can., **15**: 27-45.

Needham, P. R. 1934. Quantitative studies of stream bottom foods. Trans. Amer. Fish. Soc. **64** (1934): 238-247.

———. 1949. Survival of trout in streams. Trans. Amer. Fish. Soc., **77** (1947): 26-31.

———. 1956. The Sagehen Creek experimental wildlife and fisheries project. A.I.B.S. Bull. (Nov.): 19-21.

———, **J. W. Moffett,** and **D. W. Slater.** 1945. Fluctuations in wild brown trout populations in Convict Creek, California. J. Wildlife Mgmt., **9**: 9-25.

———, and **D. W. Slater.** 1945. Seasonal changes in growth, mortality, and condition of rainbow trout following planting. Trans. Amer. Fish. Soc., **73** (1943): 117-124.

Nielson, R. S., N. Reimers, and **H. D. Kennedy.** 1957. A six-year study of the survival and vitality of hatchery-reared trout of catchable size in Convict Creek, California. Calif. Fish and Game, **43**: 5-42.

Reimers, N. 1957. Some aspects of the relation between stream foods and trout survival. Calif. Fish and Game, **43**: 43-69.

Tack, E. 1938. Trout mortality from the formation of suspended ice crystals. Fischerei-Zeitung, **41**: 42. (Rev. in Prog. Fish Cult., 1937-1938, No. 37: 26.)

NOTES AND COMMENT

ALGAL ESTABLISHMENT ON STERILIZED SOIL REPLACED IN AN OKLAHOMA PRAIRIE[1]

This investigation is a further attempt toward understanding the algal flora of soil in an ungrazed prairie in Central Oklahoma. In particular, a relationship was sought between the natural algal flora and invasion and establishment of algae in sterilized prarie soil. The study was conducted at the University of Oklahoma Grasslands Investigations Plots, popularly known as "Johnson's Pasture." The site of the study is a tall-grass prairie, ungrazed since 1949, with a gentle north-facing slope. The area has been used for studies of soil algae by Willson and Forest (1957) and England. During the nine-month duration of this study (Jan.-Sept., 1957) the rainfall at Norman, Oklahoma was 44.46 inches. The monthly distribution is appended to Table I.

Methods

The twenty stations utilized were disposed in a grid arrangement, three east-west rows at intervals of ten yards. Each station was approximately two feet on a side with an area of four square feet. At three of the corners (sometimes four) of each station, soil samples were removed with a trowel and placed in ordinary 4½" clay pots with little disturbance. Then the potted samples were taken to the laboratory and sterilized. The pots of sterilized soil were returned to the stations and buried to ground level at the same corners from which the soil had been removed. They were buried on February 27, 1957, and a pot was collected from each station on March 31, May 31, and August 15 (at the end of one, three, and five and a half months). In addition, the visible algal crusts in the area just south of the stations were sampled occasionally, and examined immediately.

Approximately 0.5 inch of the surface soil from a pot was placed in a sterile petri plate. The top of the plate was used to remove the soil and to place the relatively undisturbed sample in the bottom half of the plate. The plate tops worked surprisingly well, but a sterile spatula would have been required had the soil been drier. The plates of soil were placed in a culture room and moistened with sterile distilled water. "Day-light" and "White" flouorescent tubes illuminated the culture at 150-300 foot candles through a 16 hour day. The temperature was maintained at 21° C., and the relative humidity at 60%. The soil samples were examined after one month incubation, and observation continued for at least a month afterward until new species failed to appear.

Presence of an alga in a plate was the only parameter utilized. The frequency percentages are based on the number of plates of the total examined (twenty, in the case of the experimental pots.) In the case of diatoms, only living ones were recorded.

It was surmised at the initiation of this study that several kinds of controls would be required. The primary comparison made was between cultures of the algal flora of the experimental pots and of the natural prairie soil of the adjoining stations. The control stations were sampled in January, April, and July, the collections being a part of Willson's unpublished investigations of the algal flora of Central Oklahoma forest and prairie soils. The control collections were taken from successive quarters of the 2′ x 2′ areas, but adjoining quarters were overlapped on each occasion. The surface was cleared of litter, and about 0.5 inch of soil was scraped off. This soil was mixed thoroughly and three plates containing about ten grams of the soil were cultured with modified Bristol's solution (Bold 1949). Since a relatively large area of surface soil was collected and mixed, and since three plates were cultured from each sample, these collections were taken to represent the "total" algal flora of the control stations.

As a check on the possibility that mixing the soil would distort the flora, plates of undisturbed soil were collected in February from the ten odd numbered stations. After culture, their flora was compared with the mixed collections.

Also examined was the possibility that the pots would alter the flora. Twelve pots of relatively undisturbed, unsterlized soil were placed at the fourth corners of the odd numbered stations and at stations 8 and 20. They were buried on March 31 and removed for culture on September 20.

Finally the sterilization procedure was tested. Sixty-six pots of soil were wrapped in glassine "sandwich" bags and autoclaved for 20 minutes, at 15 pounds pressure (approximately 121° C.). The sixty experimental pots were returned to the field and buried to ground level, and the remaining six were used as sterilization controls. Three were taken to the field, returned to the laboratory without unwrapping, and cultured. The remaining three were kept in the laboratory, then unwrapped and cultured at the end of one, two, and three months.

Results

A single individual of *Hantzschia amphioxis* was the only alga found in the six pots used to check the effectiveness of the sterilization.

Forty-two taxa were found by Willson in cultures of the natural prairie soil at the control stations, sampled in January, April, and July. Only three additional species appeared in the experimental pots, the undisturbed soil collections of February, and the pots of unsterilized soil collected in September. Only one of these, *Ulothrix bacillaris*, was found in as many as two cultures. Table I is a composite list of all species encountered and their plate frequencies. Authority for each species is given in the table but is not in the text.

In the control collections of natural prairie soil, 5 species were present at a frequency of 50% or more in January April and July, and five others attained that frequency in January and July, and six additional species in July only.

The species which showed a frequency of 50% or more in these controls were considered to be the characteristic

[1] The authors are most deeply indebted to W. T. Penfound for considerable effort in giving structure to the operation and presentation of this study. Thanks are also due R. E. Shanks, and Francis Drouet.

TABLE I. Composite list of all species encountered, with frequency for months of occurrence for those appearing in three or more collections[1]

Species	Jan.	Feb.	Mar.	Apr.	May	July	Aug.	Sept.
Anabaena oscillarioides Bory	10			10		55		
Aphanothece stagnina (Spreng.) A. Braun	20			15		50	5	
? Chlamydomonas sp.		20	10	35				
Chlorella vulgaris Beyerinck				40		40	10	
Chlorococcum humicola (Näg) Rab.	100	65	25	60	70	85	10	
Cosmarium pokornyanum (Grun.) West	10	20	10	5		20		
Cylindrospermun sp. (immature)				15	5		20	16
Cylindrospermun licheniforme (Bory) Kütz	35		20			30		
Hantzschia amphioxys (Ehr.) Grun.	100	55	25	100	100	100	80	72
Lyngbya aestuarii (Mert.) Lieb.	85	20	10	75	20	85	60	
Microcoleus paludosus (Kütz) Gom.	15	10	5	5		30		33
Microcoleus rupicola (Tild.) Drou.	10		5		5	5	5	
Microcoleus vaginatus (Vauch.) Gom.		10	5	5	10		35	48
Navicula fritschii Lund	10			10		60		
Navicula mutica Kütz.	100	100	40	100	15	100	10	66
Navicula mutica var. cohnii (Hilse) Grun.	20			15		5		
Navicula pseudatomus Lund	50			20		30		
Nostoc muscorum Kütz.	65	20	10	25	10	80	20	72
Phormidium autumnale (Agardh) Gom.	15			40	5	65	20	
Pinnularia borealis Ehr.	75	20		95		100	10	8
Pinnularia intermedia Lagerst.	80		10	10		50	15	
Plectonema nostocorum Born.	75	20	10	40	15	100	65	75
Schizothrix heufleri Grun.	15					10	5	
Scytonema hofmanni Agardh	15	10	5	5		25		8
Stauroneis muriella Lund	60			35		55	5	
Symploca muralis Kütz.	35					15	15	8
Symploca muscorum (Ag.) Gom.	65	45	20	25		55	5	8
Ulothrix flaccida Kütz.	45	10	5	20	15	60		33
Inches rainfall	1.62	.85	1.98	8.48	13.43	1.05	1.48	6.78
							June	13.19

[1] Other species: *Aphnothece muralis* (Tomasch.) Lemm., ? *Borzia trilocularis* Cohn, *Characium pringsheimii* A. Br., *Cylindrospermum majus* (Kütz) B. and F., *Cylindrospermum stagnale* (Kütz) B. and F., *Euglena* sp., *Navicula* ? *cincta* (Ehr.) Kütz., *Navicula mutica* var. *nivalis* (Ehr.) Hust., *Nitzschia* sp., *Pinnularia microstauron* (Ehr.) Cleve, *Plectonema purpureum* Gom., *Porphyrosiphon fuscus* Gom., *Porphyrosiphon notarisii* (Menegh.) Kütz., *Schizothrix purpurescens* (Kütz.) Gom., *Synechococcus aeroginosus* Näg., *Ulothrix bacillaris* (Näg.) For.

TABLE II. Frequency of algae encountered in cultures from pots of sterile soil exposed for one, three, and five and one half months, compared with algae from cultures of adjoining natural prairie

Control Plot Collections	March 31 (1 month)	May 31 (3 months)	Aug. 15 (5½ months)
Frequent species (50% or more), Jan., April, July		(percentage)	
Chlorococcum humicola	25	10	10
Hantzschia amphioxis	25	100	80
Lyngbya aestuarii	10	20	60
Navicula mutica	15		10
Pinnularia borealis		15	10
Frequent species Jan., and July			
Nostoc muscorum	10	10	15
Pinnularia intermedia	10		20
Plectonema nostocorum	15	15	65
Stauroneis muriella			5
Symploca muscorum	20		5
Frequent species July			
Anabaena oscillarioides			
Aphanothece stagnina			5
Navicula fritschii		10	
Nitzschia sp.			
Phormidium autumnale		5	20
Ulothrix flaccida	5	15	
Other species			
Chlorella vulgaris			10
Cylindrospermum sp.		5	20
Microcoleus rupicola	5	5	5
Microcoleus vaginatus	5	10	35
Schizothrix heufleri			5
Symploca muralis			15

species of the floras, and are designated the frequent species in the subsequent discussion. The 5 three-month frequent species (January, April, July) were most strongly represented in the experimental pots and in the February and September collections. The frequent species in January and July were almost as well represented. Table II shows the representation of the natural prairie soil frequent species in the experimental pots, which had been sterilized. Table III shows their representation in cultures from the unmixed soil collections from the stations (February) and from the pots of unsterilized soil (September).

In crusts collected and directly examined in February, *Symploca muscorum, Nostoc muscorum,* and *Microcoleus paludosus* were common, and *Chlorococcum humicola* and *Plectonema nostocorum* present.

DISCUSSION

It seemed unrealistic to designate any of the algae as dominants. Criteria of dominance, based on number of individuals or area coverage, were not applicable. Plate frequency, however, was easily determined and compared. It will be recalled that species of algae which were found in 50% or more of the plates from the natural prairie in a collection were recognized as the frequent species.

It was the frequent species which chiefly invaded and became established in the pots of sterilized soil. On the scale of a single growing season and at the level of plate frequency, there were no special "pioneer" algae. Colonization was effected by the commonest algae in the sur-

TABLE III. Frequency of algae encountered in cultures of unmixed, unsterilized prairie soil collected from undisturbed stations (February) and pots of unsterilized soil (September), compared with algae of natural prairie

Control Plot Collections	Unmixed prairie soil	Pots of unsterilized soil
Frequent species (50% or more), Jan., April, July	(percentage)	
Chlorococcum humicola	65	33
Hantzschia amphioxis	55	92
Lyngbya aestuarii	20	48
Navicula mutica	100	66
Pinnularia borealis		48
Frequent species Jan., and July		
Nostoc muscorum	20	72
Pinnularia intermedia		
Plectonema nostocorum	20	75
Stauroneis muriella		
Symploca muscorum	45	8
Other species		
Cosmarium pokornyanum	20	
Cylindrospermum sp.		16
Ulothrix flaccida (a frequent species in July)	10	33

rounding natural prairie. Table II shows the strong representation of those species wnich were three- and two-month frequent species in the natural prairie. The representation is a little greater after three months in the field than after one. It was predicted that cultures from the five-and-a-half month collections would resemble those from the natural prairie closely. Due to an extended delay in examining the five-and-a-half month collections, molds and bacteria began growing vigorously in the cultures. Even after their disruptive influence, the frequent species of the natural prairie were strongly represented.

A close correspondence of flora can also be seen in Table III. This was taken to indicate that neither the mixing of the natural prairie soil before culturing nor the use of pots to contain the sterilized soil affected the results of this investigation.

Although the consideration of visible crusts was a minor sidelight to this study, it seems worth noting that there is a marked difference in composition between the algal communities in the cultures from crusted soil and uncrusted soil. A few species made up the crust. *Microcoleus paludosus,* which was never a frequent species in the cultured uncrusted soil was an important crust former, while not a single three-month frequent species of the uncrusted soil was common there. Of the two three-month frequent species present, *Chlorococcum humicola* was present as an occasional single cell and *Plectonema nostocorum* was beginning to disintegrate. Diatoms, quite common in cultures of uncrusted soil, were lacking.

Generally, it may be observed that the prairie soil algae show a community realtionship that may be described as co-existence. Under the culture conditions employed, those present do not seem to interfere with others to any great extent or to occur in a regular successional sequence. Probably all of them thrive well under certain circumstances and poorly in others. When they prospered most, many prospered together. In cultures of the July collections, when the 5 three-month natural prairie frequent species were best represented (85-100%), 15 species reached the 50% frequency level, 6 of them attaining it only in that month (Table I). The "stable" prairie soil habitat is so dynamic apparently that many algae persist, with varying fortunes, over a long period of time.

SUMMARY

Cultures of algae from the surface soil in a natural prairie were compared with those from pots of sterilized soil which had been buried to ground-level and allowed to remain for one, three, and five-and-a-half months. The soil samples were cultured in moist, lighted petri plates. Only presence or absence in a plate was recorded, the frequency of a species being based on the percentage of plates in which it was found. For this study, those species which appeared in 50% of a group of plates were considered to be the frequent species.

Those species which were the most consistently frequent in the cultures from natural prairie soil also became established in the sterile soil cultures. There was no evidence of succession of different species. The cultured flora at the end of one and three months of invasion from the natural prarie approached that of the natural prairie soil cultures.

In the natural prairie soil cultures, 5 species were frequent species in all 3 samplings, 5 in 2, and 6 in one only. In the July collection there was a general abundance of many algae, the three month frequent species being present in 85-100% of the cultures. The community condition could be described as co-existence of many species.

There was no evidence that either mixing of the natural prairie soil before culturing, use of pots to contain the sterile soil, or autoclave sterilization of the pots of soil affected the composition of the cultures.

Limited direct observation of visible algal crusts in an adjacent area indicated that, while the crust formers are present in cultured uncrusted soil, the composition of the crust flora is markedly different from that of uncrusted areas. In the special circumstances of crust formation and persistence, only a few species could be said to be important.

REFERENCES

Bold, H. C. 1949. The morphology of Chlamydomonas chlamydogama, sp. nov. Bull. Torr. Bot. Club **76:** 101-108.

England, R. B. 1957. A quantitative comparison of soil algae of central Oklahoma prairie and woodland soils. Unpublished M.S. thesis, U. of Oklahoma.

Willson, D. L. and Forest, H. S. An exploratory study of soil algae. Ecology **38:** 309-313.

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RELATION OF PINE FOREST OVERSTORY OPENING DIAMETER TO GROWTH OF PINE REPRODUCTION[1]

Introduction

One of the major forestry problems in the Georgia Piedmont is how best to cut old-field pine forests so as to get adequate survival and vigorous growth of natural reproduction. More specifically, will the shade-intolerant pine seedlings make vigorous growth in openings created by single tree or group selection cuttings? Brender (1956) found that a relatively small amount of overwood markedly reduced the height growth of loblolly pine (*Pinus taeda* L.) in the lower Georgia Piedmont. According to Wahlenberg (1948), the survival and average total height growth of loblolly pine seedlings in Arkansas were best under overstory openings of 43 feet in diameter and larger. Oosting and Kramer (1946) concluded that light is a more important controlling factor than soil moisture in limiting the establishment of shortleaf pine (*Pinus echinata* Mill.) seedlings under forest stands in North Carolina. To get further information on this problem, a study was made of the relation of overstory opening diameter to the survival, height growth, and crown development of shortleaf pine and loblolly pine seedlings.

Methods

During the winter of 1951-52, a series of plots with increasing overstory opening diameters was established in a 55-year-old evenaged shortleaf pine forest with an average basal area of 145 square ft. per acre. The experiment was located on Forestry School properties in Clarke County, Georgia. The overstory openings were 5, 15, 25, 35, 45, and 55 ft. in diameter. Plots for each opening diameter class were replicated 5 times. Twenty 1-year-old nursery-grown seedlings of shortleaf pine, and 20 loblolly pine seedlings were planted with a 2 x 2 ft. spacing directly under each opening. The 5-ft. opening class was considered the control. Side lighting was negligible because of the uniform density of stocking throughout the forest. Competing ground cover vegetation was eradicated during the first 3 years. Annual recordings were made of suvival, total height, total length of needle retention on twigs per seedling, needle length, total number of branches per seedling, and stem diameter at 1 in. above ground. Average per cent of full sunlight on each plot at 4½ ft. above ground was measured with a Weston illumination meter (model 765). A 6-in. spherical globe of opal glass was attached to the light absorbing unit. All light readings were made during July and August between 10:00 a.m. and 2:00 p.m.

Table I. Annual survival of shortleaf pine and loblolly pine seedlings by opening diameter classes and average light intensity

Opening diameter	Survival for Indicated Years After Planting						Light intensity
	1	2	3	4	5	6	
Feet	*Percent*						*Percent*
	Shortleaf pine						
5	86	68	56	46	28	21	8
15	75	62	57	46	30	12	12
25	71	61	55	50	27	22	20
35	95	82	74	67	53	46	30
45	81	76	74	67	60	59	55
55	91	80	76	58	58	58	75
	Loblolly pine						
5	81	66	55	47	32	26	8
15	66	55	45	40	22	20	12
25	64	56	46	32	29	26	20
35	89	81	74	70	56	55	30
45	89	79	70	63	60	55	55
55	89	80	76	69	60	59	75

[1] Journal Paper No. 85, College Experiment Station, University of Georgia.

Results

Data on relation of opening diameter to survival of each species for a 6-year period after planting are given in Table I. The decree in survival of both species was much greater under openings of 5 to 35 feet than it was under the 45- and 55-ft. openings. It is evident from these results that the 35-ft. opening is marginal for the survival of both species. These data do show that the environmental conditions under openings of 25 ft. in diameter or less are definitely detrimental to the survival of both species.

Average light intensities for the opening classes are shown in Table I. Intensity of light increased from 8 to 75 % of full sunlight as the openings increased from 5 to 55 ft. in diameter. These data show that light intensities of 20% or less are associated with very poor survival of both species. But light intensities of 55% or higher were favorable to good survival as well as vigorous crown growth. The marginal light intensity for survival is apparently at 30%.

Average height of seedlings after planting for all plots ranged from 4.1 to 4.5 in. for shortleaf pine, and 5.4 to 6.1 in. for loblolly pine. After 6 years, the average total height had increased, in proportion to opening diameter, to from 18.6 to 66.7 in. for shortleaf pine, and from 31.2 to 111.6 in. for loblolly pine. Influence of opening diameter on height is better shown by the 5-year record of average annual increment of height growth (Fig. 1). Although the average total height did show an annual increase on all plots, the annual increment of height growth of both species actually decreased as the openings decreased from 35 to 5 ft. in diameter. But under the 45- and 55-ft. openings, the height increments showed a definite annual increase. Under the 55-ft. opening, the height increment of both species reached a peak in the third year, after which it tended to level off. According to these results, the marginal opening for height growth of both species is between 35 and 45 ft.

Opening size had a marked influence on the crown development of both species. Foliage data were not taken after the fourth year because it became impractical to measure the crowns grown under the 2 largest openings. During the first 4 years, the average total number of branches per seedling had increased, in proportion to opening diameter, to from 3 to 13 for shortleaf pine, and from 3 to 15 for loblolly pine. An increase in branch growth was in turn associated with an increase in the average total length of needle retention on the branches. All measurements were made in the fall after the 3-year-old needles had been shed. Data on the relation of the annual increase in needle retention to opening diameter classes are shown in Figure 2. The length of needle retention for shortleaf pine increased from only 5 to 22 in. as the openings increased from 5 to 35 feet, whereas, it was 45 and 78 in. under the 45- and 55-foot

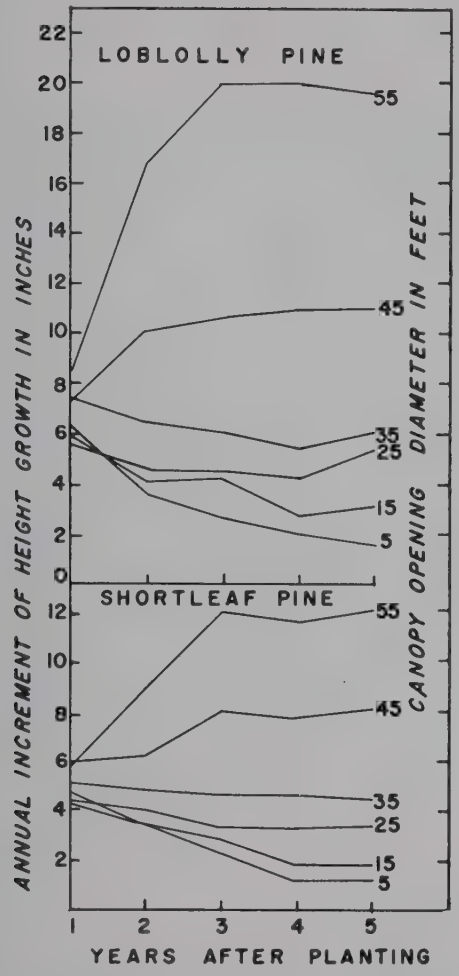

FIG. 1. Relation of overstory opening diameter to the average increment of height growth of shortleaf pine and loblolly pine.

openings, respectively. For loblolly pine, the increase was from only 4 to 25 in. under openings of 5 to 35 feet, whereas, it was 54 and 111 in. under openings of 45 and 55 feet, respectively. These data show that an opening of at least 45 feet in diameter is necessary for adequate foliage growth of both species.

An increase in crown growth was associated with an increase in average stem diameter (Fig. 3). For shortleaf pine, the stem diameter increased from only 5.6 to 10.5 mm as the openings increased from 5 to 35 ft., as compared to 18.4 and 24.8 mm under the 45- and 55-ft. openings. The stem diameter of loblolly pine increased from only 8.2 to 14.4 mm under openings of 5 to 35 ft., as compared to 21.8 and 35.9 mm under the 45- and 55-ft. openings.

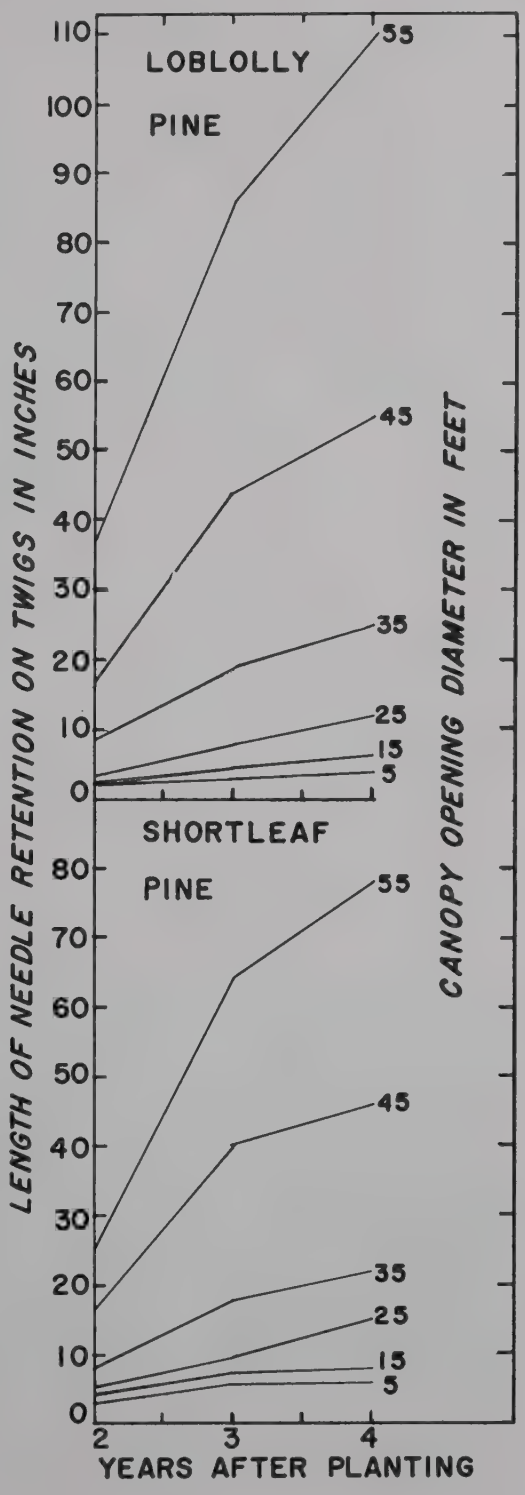

FIG. 2. Relation of overstory opening diameter to the average total length of needle retention on the twigs of shortleaf pine and loblolly pine.

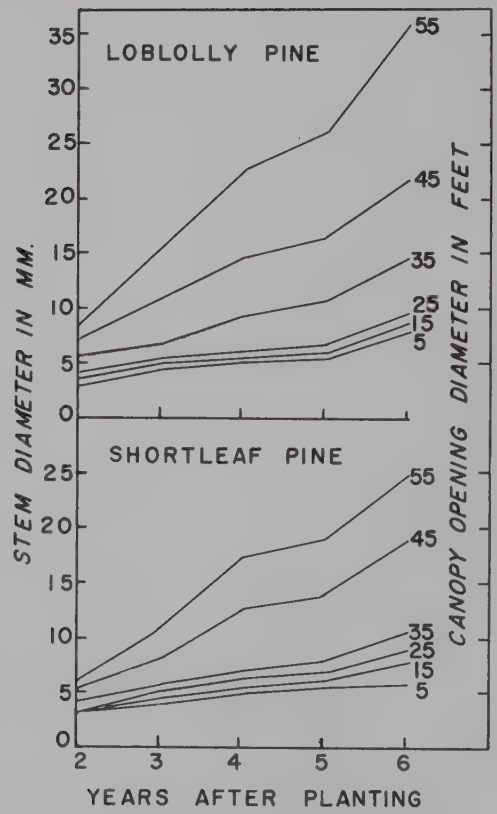

FIG. 3. Relation of overstory opening diameter to average stem diameter, at 1 inch above ground, for shortleaf pine and loblolly pine.

SUMMARY

During the winter of 1951-52, an experiment was established on the survival and growth of shortleaf pine and loblolly pine seedlings under six forest overstory opening diameter classes that increased by 10-ft. intervals from 5 to 55 ft.

After 6 years, the average survival of both species varied from only 12 to 31% under the 5 to 25 ft. openings, as compared to 46 to 59% under the 35- to 55-ft. openings.

During the first 5 years, the increment of annual height growth of both species actually decreased as the openings decreased from 35 to 5 ft., whereas, it increased rapidly under the 45- and 55-ft. openings.

Over a 5-year period, the increase in average number of branches per seedling, in proportion to the size of the opening, ranged from 3 to 13 for shortleaf pine, and 3 to 15 for loblolly pine.

Over a 4-year period, the average length of needle retention for both species increased from only 4.0 to 25.1 in. under the 5- to 35-ft. openings, whereas, it was 45.0 and 78.0 in. for shortleaf pine, and 54.0 and 111.0 in. for loblolly pine, under the 45- and 55-ft. openings, respectively.

For shortleaf pine, the annual stem diameter growth increased from only 5.6 to 10.5 mm under the opening classes of 5 to 35 ft., as compared to 18.4 and 24.8 mm under the 45- and 55-ft. openings. The increase for loblolly pine was only from 9.2 to 14.4 mm under the 4 smaller openings, as compared to 21.8 and 35.9 mm under the 2 large openings.

REFERENCES

Brender, E. V. and J. C. Barber. 1956. Influence of loblolly pine overwood on advance reproduction. Southeastern Forest Exp. Sta. Paper No. 62. 12 pp.

Oosting, H. J. and P. J. Kramer. 1946. Water and light in relation to pine reproduction. Ecology 27: 47-53.

Wahlenberg, W. G. 1948. Effect of forest shade and openings on loblolly pine seedlings. Journal Forestry 46: 832-834.

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MISSING ANNUAL RINGS IN BRANCHES OF YOUNG-GROWTH DOUGLAS-FIR

A striking lack of agreement between the number of annual rings in the bases of live branches and in tree stems at their points of intersection was observed during a study[1] of normal crown die-off in young-growth Douglas-fir in the summer and fall of 1956.

Seven trees, ranging in age from 35 to 70 years (5 were in the 50- to 60-year age class), were analyzed. Five were located on McCleary Experimental Forest,[2] near McCleary, Wash., and 2 were on the University of Washington's Lee Forest, near Maltby, Wash. When the first tree was pruned, ring counts showed 8 to 10 fewer rings in branches in the lower whorls of the live crown than in the bole at the points where bole and branches intersected. Bole age was determined both by ring counts at various heights on the stem, either through increment borings or direct counts on stem sections, and by counting nodes. Similar discrepancies were observed in the lower live branches of subsequent study trees.

The difference between bole age and apparent branch age ran as high as 15 years on one tree. Although generally smaller, discrepancies of 9 or 10 rings were not uncommon. There were no observed external indications,

[1] Carried out by the writer for a thesis entitled "A study of the interrelationships between growing space, crown development, and stem development of second-growth Douglas-fir", presented in partial fulfillment of the requirements for the degree of Master of Forestry at the University of Washington.

[2] Maintained in cooperation with Simpson Logging Co.

other than the position of the branches in the crown, that the branches should be growing poorly. In all cases, foliage was plentiful and appeared healthy.

Branch cross-sections were polished and growth rings were examined with the aid of a low-power lens. Because

FIG. 1. A typical branch section from a young-growth Douglas-fir. Note the variation in ring width and in number of obvious rings in the outer area (outside the ring shown by the dash line). The top of the branch is at the top of the picture.

growth rings near the cambium were incomplete, the part of each cross-section showing the greatest number of rings was selected for ring counts. In most cases these outer rings were widest, as well as most numerous, on or near the upper side of the branch, despite the fact that the rings laid down earlier in the branch's life were generally narrower there (Fig. 1).

DISCUSSION

Where discrepancies exist, branches either are younger than the nodes at which they occur or have failed to differentiate growth rings. Radial growth of the bole would engulf no more than the first year's branch elongation, as initial elongation is normally sufficient to extend the branch tip beyond the point of engulfment. Since the formation of epicormic branches on Douglas-fir is uncommon, and since most of the branches studied were obviously of axial origin, epicormic branches could account for the discrepancy in only a very limited number of cases. Therefore, it seems logical to conclude that the branch simply did not form a distinguishable growth ring at its base every year. Furthermore, since incomplete rings are evident only near the cambium, the failure to form growth rings probably takes place during this terminal period and may be an indication of approaching death.

These observations and conclusions are in accordance with findings in other species. Andrews and Gill (1939), working with ponderosa pine, found such discrepancies to exist in a large number of cases. They found the frequency and magnitude of the discrepancies to be correlated with the relative position of the branches in the crown, both quantities tending to decrease as the height above the lowest living branch increased. They concluded, therefore, that discrepancies are most likely to occur after branches have passed their physiological prime and have entered into the period of suppression that ordinarily precedes death. Romell (1937, 1940-41) found in Scotch pine and Norway spruce that for a number of years before the branches die, they do not form annual rings. He also found that the frequency and magnitude of the discrepancy decreased with increasing depth into the live crown. He observed that a bundle of up to 10 or more annual rings in the stemwood, bending out toward the knot, may narrow into nothing and lead into the surface layer of the branchwood. Similar observations are quite commonly noted on suppressed trees and branches.

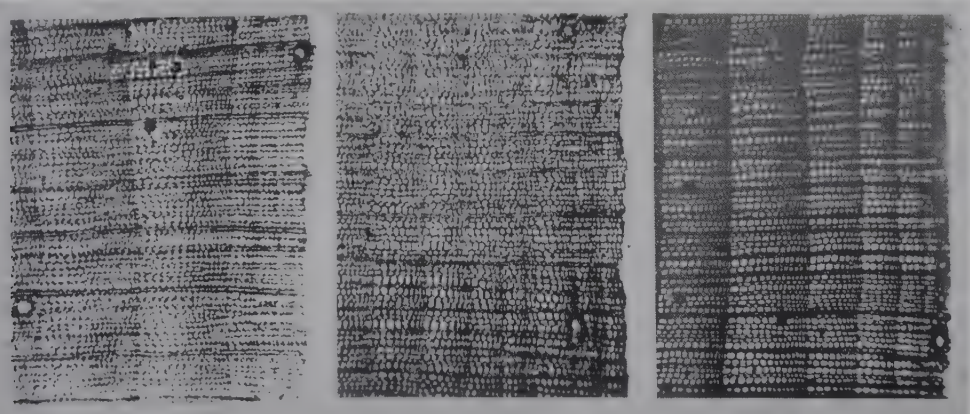

FIG. 2. Microslides made from selected branch sections show the variation in the pattern of ring formation during the latter years of branch life. The right edge of each phtograph is the cambium of the branch cross-section, with the rings proceeding from left to right.

The apparent failure of branches to form growth rings could be explained in two ways: (1) cell formation ceased during the latter years of the branch's life, or (2) cambial activity was so slight at this time that the rings are only one or two cells wide and no differentiation into springwood and summerwood has occurred. Although there is no proof as to which is the case, the latter explanation seems most logical. Microsections were made from some of these branches to be certain that the rings were really missing, and not miscounted due to insufficient magnification (Fig. 2). One branch that appeared to have 9 fewer rings than it should showed only 11 rows of cells beyond the last distinguishable ring.

A significant inference is that lower branches contribute little or nothing to tree development. If this is the case, it may be an argument in favor of pruning live branches from young-growth Douglas-fir. There is a possibility that production may even be raised by pruning these branches. This inference is in accordance with Stein's (1955) findings in Douglas-fir that pruning lower live branches may increase tree growth slightly. In recent years, European foresters have debated whether or not lower limbs place a drain on tree growth. It is evident, however, that a more definitive experiment is needed to provide a conclusive answer.

References

Andrews, S. R. and Gill, L. S. 1939. Determining the time branches on living trees have been dead. Jour. Forestry **37**: 930-935.

Romell, Lars-Gunnar. 1937. Kvistrensning och övervallning hos okvistad och torrkvistad tall. Svenska Skogsvårdsföreningens Tidskrift **35**: 299-328.

———. 1940-41. Kvistningsstudier å tall och gran. Meddelanden Från Statens Skogsförsöksanstalt **32**: 143-194.

Stein, W. I. 1955. Pruning to different heights in young Douglas-fir. Jour. Forestry **53**: 352-355.

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PRESENCE AND COVER IN PITCH PINE–OAK STANDS OF THE SHAWANGUNK MOUNTAINS, NEW YORK

Introduction

The similarity of the ridge top vegetation of the Shawangunk Mountains to that of the pine-barrens of New Jersey and the sand plains of New York has been noted by several authors. (Bray 1930, Harshberger 1911, Torrey 1932). Some have commented on the occurence of species of coastal plain or boreal distributions on these same ridges and have briefly noted some of the plant species encountered (Britton 1883, Redfield 1884, Torrey 1932, 1935). Although considerable interest has been evidenced in the flora of the summit of the Shawangunk's, quantitative analysis of the vegetation is lacking. In this paper the composition of the pitch pine-oak (*Pinus rigida Mill.—Quercus prinus L.*) forest is summarized by means of presence data, and the cover relations of tree and shrub layers in two stands are presented.

The Shawangunk Mountains are located in Ulster County, southeastern New York State. Physiographically they are part of the Ridge—Valley Province and consist of a cap of hard Shawangunk conglomerate over Hudson River shales. The conglomerate, on which most of the pitch pine-oak stands occur, is comprised of quartzite pebbles in a silicaceous matrix (Darton 1893). The entire region was glaciated in the Pleistocene. Rock outcroppings are common and soil development is limited, the soil consisting of a shallow layer (2"-8"), largely of accumulated organic matter lying on bedrock.

The stands examined are found at altitudes ranging from 1250 feet to 2200 feet above sea level which approaches the highest altitude in this range. They are located in an area between highways 55-44 on the north to highway 52 on the south, or roughly from the vicinity of Lake Minnewaska to Cragsmoor. The nearest climatic data come from Mohonk Lake at an altitude of approximately 1200 feet and several miles to the north. The mean January and July temperatures are 25.1° F and 69.9° F respectively. The extremes of temperature in a thirty nine year period of record are —24° F minimum and 96° F maximum. Average precipitation is 46.8 inches. The area is included in the Oak-Chestnut Forest Region of Braun (1950); or the Chestnut, Oak Hickory (Zone B) of Bray (1930). Much of the range is covered by mixed hardwood forest dominated by oak species although a northern hardwood forest including sugar maple, beech, and hemlock is found on mesic slopes and in coves. The exposed ridges and xeric slopes are commonly covered by rather scrubby, open canopied forests composed chiefly of pitch pine and oak which grade into mixed oak forests. In one instance an extensive flat-topped summit is covered with a dwarfed stand of pitch pine having the physiognomy of a tree line forest although the altitude is well below that at which the tree line is usually found in this region.

I wish to express my appreciation to Mrs. Inez Haring and Dr. T. C. Frye for determination of mosses and liverworts.

Methods

An initial survey of the region was made and presence lists compiled for eight separate stands chosen on the basis of the presence of pitch pine and location on an exposed slope or ridge. Each stand was visited twice at different times during the summers of 1956 and 1957. Two stands were sampled by the line intercept method to determine the cover of the tree and shrub layers. One, predominantly pine, was located along a ridge (ca 1400 ft) oriented in a northeast to southwest direction. The other, predominantly oak, was located nearby (ca 1350 ft) on a slope facing northwest. In these two the tree canopy was sampled by five lines, each forty meters in length. The lines were separated by a distance of twenty meters. The shrub cover was sampled by four one meter lines in each forty meters. These were arbitrarily located at every tenth meter. Thus, a total of two hun-

dred meters linear distance was sampled for tree cover in each stand and ten per cent or twenty meters sampled for shrub cover. The canopy of each individual was determined separately by visually projecting a perpendicular from its periphery to the point where it intersected the line on the ground. The canopy of trees was measured to the nearest decimeter, the shrub cover to the nearest centimeter. Cover as used here, refers to the linear extent of the canopy. Nomenclature of the vascular plants follows Gleason (1952), that of mosses follows Grout (1940). Voucher specimens are in The Nieuwland Herbarium at The University of Notre Dame.

Results

Presence

In the eight areas sampled for presence a total of twenty one tree species, eighteen shrub species and eighteen herbaceous species were encountered. Only twelve species of trees, twelve shrub species and seven herbaceous species were encountered in at least 50% of the stands. (Table I) The subjective homogeneity of

Table I. Tree, shrub and herb species present in at least 50 percent of the stands

Trees	% Presence
Acer rubrum L.	75.0
Amelanchier arborea (Mich.f.) Fern.	50.0
A. laevis Wieg.	50.0
Betula lenta L.	62.5
B. populifolia Marsh.	75.0
Castanea dentata (Marsh.) Borkh.	75.0
Nyssa sylvatica Marsh.	62.5
Pinus rigida Mill.	100.0
Quercus coccinea Muenchh.	50.0
Q. prinus L.	87.5
Sassafras albidum (Nutt.) Nees.	87.5
Tsuga canadensis (L.) Carr.	75.0
Shrubs	
Aronia melanocarpa (Michx.) Ell.	75.0
Gaylussacia baccata (Wang.) K. Koch.	87.5
Hamamelis virginia L.	50.0
Kalmia angustifolia L.	75.0
K. latifolia L.	87.5
Myrica asplenifolia L.	75.0
Quercus ilicifolia Wang.	100.0
Rubus hispidus L.	62.5
Vaccinium angustifolium Ait.	100.0
V. corymbosum L.	50.0
V. vacillans Torr.	75.0
Viburnum cassinoides L.	50.0
Herbs	
Arenaria groenlandica (Retz.) Spreng.	62.5
Epigaea repens L.	50.0
Gaultheria procumbens L.	100.0
Maianthemum canadense Desf.	50.0
Melampyrum lineare Desr.	62.5
Pteridium aquilinum (L.) Kuhn.	100.0

the stands is due to the fact that a very limited number of species constitute a large proportion of the total vegetative cover rather than to extreme floristic similarity. Several species (*Nyssa sylvatica* Marsh., *Sassafras albidum* (Nutt.) Nees., *Castanea dentata* (Marsh.) Borkh.), although commonly present, constitute only a negligible fraction of the total vegetative cover. The paucity of herbaceous species is evidenced by the limited number of species and by their sparse distribution in the stands. This very limited herbaceous layer is in accord with the findings of Buell and Cantlon (1950) in a study of pine-oak forest in the New Jersey Pine Barrens. The similarity of the Shawangunk vegetation with that of the Pine Barrens, which has been noted, is a physiognomic similarity rather than a floristic one, and although many species are found in common these are usually wide ranging plants common to xeric habitats. The Shawangunk stands are less rich in species and do not include most of the species most characteristic of the Pine Barrens. They are akin to the heath shrub aspect of the Plattsburg Sand Barrens (Bray 1930). In general appearance and early successional stages these stands are similar to the pine stands and xerarch succession described by Niering (1953) in the Kittatinny Mountains of New Jersey. The importance of crevices as starting places for the vegetation mats which spread at the periphery over the bare rock is particularly noted. Mosses play a prominent role in these mats and, although no comprehensive survey was made of these, the following species were encountered: *Polytrichum commune* Hedw., *P. juniperinum* Hedw., *P. piliferum* Hedw., *Leucobryum glaucum* (Hedw.) Schimp., *Distichum capillaceum* Hedw. *Gymnocolea inflata* (Huds.) Dumort., a liverwort, was also collected.

Ring counts indicate that the largest pitch pines are approximately fifty years old. These trees are marked by a strongly twisted trunk growth.

Cover

Of the two stands selected for more detailed analysis the one with a larger component of pitch pine has a more open canopy, over one half of the total sample being recorded as open space (Table II). Although the density

Table II. Tree density and average per cent of linear distance covered

Species	Pine Stand		Oak Stand	
	Density	% Cover	Density	% Cover
Pinus rigida	19	22.4	9	9.7
Quercus prinus	11	22.2	26	48.9
Acer rubrum	2	1.3	3	4.3
Quercus velutina Lam.	1	1.5	2	3.1
Tsuga canadensis	0	0.0	1	0.9
Amelanchier sp.	0	0.0	7	5.6
Open space	—	55.3	—	34.5

of pine is greater than that of oak the broader canopy of the oaks gives them almost as large a cover percentage. Other tree species are a minor component comprising a total cover of only 2.8 per cent. The height of the canopy is only 15-20 feet although a few individual pines in the vicinity which were not included in the sample exceeded this range. It seems most probable that these are relics of an earlier stand destroyed by one of the fires which occur commonly. The shrub layer is discontinuous and composed largely of blueberry (*Vaccinium angustifolium* Ait., and huckleberry *Gaylussacia baccata* (Wang.) K. Koch) Table III). Considerable areas of bare rock are exposed.

The second stand is principally oak both in density and cover. A larger portion of the tree canopy (13.9%) is made up of other than chestnut oak and pitch pine. The canopy is slightly higher than the pine stand, approximating 25 feet. The shrub understory is more nearly

TABLE III. Average per cent of linear distance covered by shrubs

Species	Pine Stand	Oak Stand
Vaccinium angustifolium	31.9	4.9
V. vacillans	0.0	11.8
Gaylussacia baccata	12.1	45.9
Quercus ilicifolia	2.2	0.2
Amelanchier sp.	1.7	0.7
Hamamelis virginianum	1.2	0.0
Kalmia latifolia	5.0	12.2
Open space	55.2	28.9

continuous and is somewhat taller. *Vaccinium angustifolium* is less important in the shrub layer and *Gaylussacia baccata* is substantially more important, constituting nearly one half of the linear cover.

If the individual subsamples of the stands are taken as a composite of the pitch pine-oak forests and arranged in order of increasing open space in the tree canopy, the oak cover is seen to diminish while the pine cover increases; and as the total open space in the tree canopy increases the shrub cover decreases (Fig. 1).

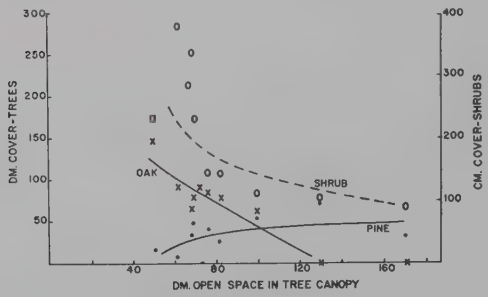

FIG. 1. Relationship of tree and shrub cover to open space in the tree canopy. Left hand scale is decimeters covered by trees (X-chestnut oak, dots-pine). Right hand scale is centimeters of total shrub cover.

In neither stand was the herbaceous layer significant. In the initial samples the herbaceous cover was so sparse that sampling was discontinued. *Gaultheria procumbens L.* and *Epigaea repens L.* were encountered occasionally as a ground layer.

DISCUSSION

The physiognomic similarity of the pine-oak forest of the summit of the Shawangunk Mountains and that of the Pine Barrens of New Jersey, which has been noted by various botanists, is emphasized by the use of quantitative measures. Although the flora of the Pine Barrens includes many species not found in the Shawangunks, the composition of the most important species of the tree layer is quite similar. The "Index of Similarity" described by Bray and Curtis (1957) was used to compare the stands studied here with those studied in the Pine Barrens by Buell and Cantlon (1950). This index simply sums the lower values of a relative measure, e.g. per cent density or per cent cover, for those species which have a measured value in both of the stands being compared. Thus, if two stands had exactly the same values for the same species the index would be 100; if no species were present in common the index would be 0. When the pine stand of this paper is compared with the New Jersey pine stand of Buell and Cantlon, and an index is calculated based on relative density as sampled by transect, the index value is 60. If the oak stand of this paper is compared with the oak stand described by Buell and Cantlon the index value is 64. These values are more meaningful if it is noted that Bray and Curtis found that the mean index value of seven replicate samples taken in the same stand was 82, although this value would vary with the intensity of sampling. The fact that of nine species present in the first pair of stands only two were common to both was overshadowed in the index because these two constituted a large portion of both stands.

If a similar index is calculated for the shrub layer using per cent cover as a basis the index value for the pine stands is only 27. This smaller value is due principally to the presence of different species of Vaccinium and to the presence of *Gaylussacia frondosa (L.) T&G.* in the Pine Barrens stand and its absence from the Shawangunk stand, which has a larger proportion of *Gaylussacia baccata*. Such substitution of species having similar habit would have little effect upon the physiognomy of the stand. The shrub layer index for the pair of stands predominantly of oak was 57. Ideally the use of such values as the index of similarity would be based on identical sampling techniques and intensity. In this case, although the sampling methods are comparable, the data of Buell and Cantlon are based on a substantially larger sample. It is of interest to note that the index of similarity values for the two stands of the present study are 62 based on relative density of trees and 40 based on relative cover of shrubs. The index of similarity value based on relative density of trees in the two stands from the Pine Barrens is 31.3 while that based on relative cover of shrubs is 58. The Shawangunk stands are more similar to each other in tree composition and less similar in shrub composition while the reverse is the case in the two stands described by Buell and Cantlon.

In a study of the vegetation of High Point State Park in the Kittatinny Mountains of New Jersey, Niering (1953) described stands of pine and oak. The Kittatinny range is continuous with the Shawangunks and similar geologically. The general appearance and succession of the vegetation of the ridges is very similar. The stands encountered in the Shawangunks, however, consist of various mixtures of pitch pine and chestnut oak while those reported by Niering for the Kittatinny Mountains are mixtures of pitch pine and scarlet and white oaks (*Quercus coccinea Muenchh.* and *Quercus alba L.*), chestnut oak being only a minor component. *Quercus ilicifolia Wang.* is also less prominent in the Shawangunk stands. These apparent differences may be due to the chance variation of the stands selected for sampling but it is possible that the species may behave differently, even in areas so proximate and similar to each other.

SUMMARY

The physiognomic similarity of pitch pine-chestnut oak stands of the Shawangunk Mountains of New York and the pine-oak forests of the Pine Barrens of New Jersey is discussed and is emphasized by quantitative measures. In spite of marked floristic differences the most important species of trees are common to both (*Pinus rigida* and *Quercus prinus*). The ericaceous shrub layer was predominantly composed of species of Vaccinium and Gay-

lussacia in varying proportions. The herbaceous layer was sparse in both. Similar forests in the contiguous Kittatinny Mountains of New Jersey include mixtures of pitch pine and white and scarlet oaks in lieu of the chestnut oak found in the Shawangunk's.

References

Braun, E. Lucy. 1950. Deciduous forests of eastern North America. Philadelphia: Blakiston Co.

Bray, W. H. 1930. The development of the vegetation of New York State. N. Y. State Col. Forestry Tech. Publ. 29.

——— **and J. T. Curtis.** 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monog. 27: 325-349.

Britton, N. L. 1883. Notes on a botanical excursion to Sam's Point, Ulster Co., N. Y. Torrey Bot. Club. Bull. 10: 105.

Buell, M. F. & J. E. Cantlon. 1950. A study of two communities of the New Jersey Pine Barrens and a comparison of methods. Ecology 31: 567-586.

Darton, N. H. 1893. Preliminary report on the geology of Ulster County. Report of the State Geologist of New York for 1893.

Gleason, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Lancaster, Penna.: Lancaster Press.

Grout, A. J. 1940. Moss flora of North America. Newfane, Vt.

Harshberger, J. W. 1911. A phytogeographical Survey of North America. G. E. Stechert, N. Y.

Niering, W. A. 1953. The past and present vegetation of High Point State Park. New Jersey. Ecological Monog. 23: 127-148.

Redfield, J. H. 1884. *Corema conradii and its localities.* Torrey Bot. Club. Bull. 11: 97-101.

Torrey, R. H. 1932. More stations for *Potentilla tridentata.* Torreya 32: 159-161.

———. 1932. The *Corema conradii* station on Shawangunk Mountain. Torreya 32: 97-100.

———. 1935. Trip of Sept. 21-22 in the Shwangunks. Torreya 35: 153-155.

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WEATHERING CHARACTERISTICS OF DECIDUOUS LEAF LITTER

Introduction

An inspection of the leaf litter under a deciduous forest stand generally indicates varying stages of decomposition. Some leaf specimens appear relatively intact, several months after leaf drop, while others of the same age show advanced weathering. Climatic intensities and length of exposure time are variables in rate of weathering; however, the chemical composition of leaves is also a factor.

Composition of leaves varies with species although it may be modified to some extent by variations in site. Daubenmire (1953), in Rocky Mountain studies, concluded, however, that leaf composition varied primarily on the basis of the individual species. In the study of oak litter in Ohio, Finn (1953) indicated that foliar potassium and phosphorus were independent of site, although foliar nitrogen and calcium were modified by soil conditions. Total leaf ash of several hardwoods in Iowa was generally consistent for each species, although physiographic and erosional differences existed in the sites (Kucera, 1950). Based on data compiled from numerous sources, Lutz (1946) concluded that specific variations in the chemical composition of leaves are important, in addition to environmental influences.

Leaf composition also varies with length of exposure. As mineralization progresses, ash content based on percentage dry matter generally increases. This is a relative value based on reduction of the organic fraction proceeding at a faster rate than leaching losses in ash. Tenney and Waksman (1929) indicated that the relative amounts of water soluble and more resistant substances were critical in regulating the speed of break-down. Mineral properties of the foliage over a period of time might be an index of the break-down process. Such evaluations, all other factors being equal, possibly are significant in comparing species reaction on nutrient turnover and soil fertility.

The present study was undertaken to determine under equable physical conditions what differences exist between several deciduous species in weathering characteristics of the leaf litter.

Procedures

Leaf materials of six forest species were used in this study. These were *Quercus alba,*[1] white oak; *Q. rubra,* northern red oak; *Q. marilandica,* black-jack oak; *Acer saccharum,* sugar maple; *Carya ovata,* shagbark hickory; and *Ulmus americana,* American elm. All samples were obtained from native forest stands in Boone County in Central Missouri. The terrain of the collection areas is characterized by steep slopes of 15 to 30 per cent. Soils are generally thin and stony. The parent material is a cherty limestone of the Burlington Formation, Mississippian Series, occurring as massive outcroppings. In order to minimize the site factor, collections were made in locations with the greatest uniformity in soil depth, slope, and aspect. It was possible to obtain adequate samples of all species within generally narrow spatial limits, although the particular site could not be considered average for all species. This applied particularly to the elm which occurs in greater abundance on the lower slopes and in the stream bottoms.

Approximately 180 to 200 grams of fresh leaves from each of two locations were collected in the fall of 1956. Sampling was done from several trees in each site at the time leaves were turning color and starting to fall. These unweathered collections were divided into five lots for each species from each of the two sampling areas,

[1] Nomenclature follows Gray's Manual of Botany, ed. 8, 1950.

making a total of 60 species subsamples. One set of subsamples, from each site, was oven-dried and an average ash content determined for the unweathered condition. The remaining subsamples consisting of approximately 30 to 35 grams were placed in lath frames with top and bottom of aluminum screen. These boxes were returned to the original site and placed on the forest floor. One species subsample at each of the two locations was taken up at the end of 4, 8, 12, and 18 months. Leaves which appeared dusty were not used. The remainder from each subsample was dried to permit grinding. Ground materials from each site were then oven-dried at 100°C. and duplicate samples of approximately 3 to 4 grams were ashed at 500°C. (Piper 1947). Total ash for each species was based on an average of the two sites. Midway between each ashing date boxes remaining in the field were turned over to expose the underside. Since the leaf stalks of maple and hickory comprised a high proportion of the total leaf weight, compared with the other species, analyses were conducted separately for the blades and stalks of these two trees. Maple petioles averaged 12.9 per cent of total leaf weight, and hickory leaf stalks, including the rachis, 21.0 per cent.

Potassium for white oak, maple, and elm was analyzed by flame photometric method.[2] For this, the total ash samples previously determined for different periods of leaf weathering were used. In addition, total ash samples derived from litter after only 30 days were also analyzed for potassium. This usually abundant cation occurs in plants mainly in soluble form. The relatively rapid decomposition of some leaf types might also be accompanied by a parallel loss of this ion. The purpose of the determination was to observe a possible relationship between any such loss and leaf weathering. For these three species, the loss of soluble products from fresh leaves by hot water extract was also determined at intervals over a 30 day period. A cork borer was used in cutting equal-area samples for duplicate tests of 100 cuttings each. These were dried, weighed, and immersed in distilled water at 60°C. Leachates were decanted at the end of 2, 10, 20, and 30 days. At the end of each period, the samples were rinsed, dried, and weighed to determine percentage losses of soluble matter. Each sample was again soaked in fresh water and returned to the oven for the selected interval.

Results

Leaf ash values differed for the six species, and increased with time of exposure (Table I). On the basis of total mineral content, the species were resolved generally into two groups. The three oaks had lower values than elm, hickory and sugar maple. In the low ash group, black-jack oak showed the least mineral content per unit weight of dry matter, and elm was superior in the high ash group.

All values increased steadily during the period of weathering. Changes in the physical conditions of the litter samples also occurred. The most apparent differences were observed in the leaves of elm. After 18 months, the leaves were fragmented and crumbled readily in the process of handling. The weathering of elm leaves probably is augmented by this crumbling effect, since the surface exposed to weathering would be increased. The least obvious change during the period was shown in the oaks. The litter of these species was mostly intact. From these observations, some measure of relationship is suggested between initial mineral levels and the subsequent weathering history. Where mineral level is high, loss of leaf character is relatively rapid. In the case of the oak species, which have the least mineral matter on a dry weight basis, the break-down process is noticeably retarded. Similar observations can be made in the same species when comparing data of petioles and foliar tissue for maple and hickory. The larger organic fraction, a part of which is insoluble, would seem to be a factor. Tenney and Waksman, previously cited, indicated that the proportionality of the soluble and insoluble fractions was critical in determining the rate of decomposition. Leaves of yellow oak had a very high lignin content, 75% of which remained after 386 days of incubation.

Losses of water soluble products from fresh leaves of elm, white oak and sugar maple are shown in Table II.

Table I. Total mineral content as per cent of dry leaf matter for different tree species with increasing lengths of exposure under field conditions

Species	Months After Leaf Drop and Corresponding Season of Year				
	0 Nov. '56	4 Mar. '57	8 July '57	12 Nov. '57	18 May '58
American Elm	13.81	16.40	18.00	21.32	31.17
Sugar Maple	8.82	11.51	17.50	24.95	27.75
S.M. petiole	3.37	4.71	7.30	.....	10.78
Shagbark Hickory	9.73	11.25	18.72	21.20	27.43
S.H. petiole and rachis	5.52	5.90	8.00	.....	11.11
N. Red Oak	3.85	6.67	9.23	11.71	16.15
White Oak	4.25	6.50	9.91	11.52	15.51
Black-jack Oak	2.67	4.23	6.30	7.15	12.60

Table II. Percentages losses in dry leaf weight after varying periods of leaching by hot water (60°C)

Species	Days of Leaching				Total Loss
	2	10	20	30	%
American Elm	32.81	8.24	2.25	3.05	46.35
Sugar Maple	28.90	7.15	2.55	2.50	41.10
White Oak	26.60	5.75	2.51	1.95	36.81

As discussed previously, these samples were equated on an area basis, thus eliminating the variable of weathering surface. Reductions in dry weight upon leaching were greatest in elm, followed by sugar maple and white oak. At the end of 30 days, elm litter had an accumulated loss based on the initial dry weight of equal-area samples of 46.35%. This is approximately 21% more than losses in white oak and exceeded that for sugar maple by 13%. These variations are in accord with differences observed in relative weatherability of these species. Although reductions in dry matter varied according to source of litter, the percentage of the respective 30-day totals occurring after two days did not. This value was approximately 70% for each species. At the end of the first 10-day period, the percentage averaged 90% for the three types of litter. Thereafter, additional increments were small and approximate. This would suggest that the bulk of water-soluble products is lost rather rapidly following leaf drop under natural

[2] Analyses were made by the Spectrographic Laboratory, University of Missouri.

conditions, and that prolonged leaf stability is based on the remaining insoluble part. In the case of elm litter with a smaller insoluble fraction less stability in indicated.

Potassium in leaves, expressed as per cent K content of dry matter, varied for the species which were studied. For fresh-picked leaves of elm, sugar maple, and white oak, the percentages were respectively 1.29, 0.80, and 0.67. Potassium was leached readily under field conditions, as might be expected. After 30 days these values, in order, had dropped to 0.14, 0.37, and 0.41, indicating the most rapid losses for elm, and the least for oak. At the end of the fourth month, in March, potassium contents were less variable, ranging from 0.085% for oak to 0.110% for maple. Thereafter, through the eighth, twelfth, and eighteenth months variations were insignificant. The rapid decline in potassium in the initial phases of weathering was similarly observed by Lunt (1933), who showed an 80% reduction in beech leaves after eight weeks.

Although potassium is lost rapidly, relative increases in total ash occur during the same period of weathering and indicate the greater stability of other mineral constituents.

Summary

1. Weathering studies were conducted over an 18 month period for six deciduous species: American elm, sugar maple, shagbark hickory, white oak, northern red oak, and blackjack oak.

2. Criteria employed were changes in total mineral content determined at four month intervals, leaching losses of water-soluble matter from equal-area samples in the laboratory, and potassium decrease under field conditions.

3. Generally, the oaks were classed in the low-ash group, elm, sugar maple, and hickory in the high-ash group.

4. Superficial observations based on appearance and physical condition would indicate greater resistance to weathering for the oaks as a group, and the least for elm. Maple litter appeared more stable than that of hickory.

5. These observations correlated with the analyses which were made, to the effect that the more resistant oak litter had less total mineral, less soluble materials as determined by hotwater extraction, and the least decrease in potassium in the initial weathering phase. This was in contrast to the more weatherable elm litter which had a high mineral level, more soluble product, and the greatest initial drop in potassium.

6. In evaluating species reaction on the nutrient cycle, the study would suggest elm as the most effective in rapid turn-over.

References

Daubenmire, R. 1953. Nutrient content of leaf litter of trees in the northern Rocky Mountains. Ecology **34**: 786-793.

Finn, R. A. 1953. Mineral content of leaves clue to white oak site quality. Tech. Paper No. **135**. Central States Forest Expt. Station. Columbus, Ohio.

Kucera, Clair. 1950. An ecological study of a hardwood forest area in Central Iowa. Ecological Monog. **22**: 283-299.

Lunt, H. A. 1935. Effect of weathering upon dry matter and composition of hardwood leaves. Jour. Forestry **33**: 607-609.

Lutz, H. J. 1946. Forest Soils. John Wiley & Sons, Inc. New York.

Piper, C. S. 1947. Soil and Plant Analysis. Interscience Publishers, Inc. New York.

Tenney, F. G. and S. A. Waksman. 1929. Composition of natural organic materials and their decomposition in the soil: IV. Soil Science **28**: 55-84.

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LONGEVITY OF STORED JUNIPER SEEDS[1]

Germination tests were done with various-age stored seeds of alligator (*Juniperus deppeana* Steud.), one-seed (*J. monosperma* (Engelm.) Sarg.), and Utah juniper (*J. osteosperma* (Torr.) Little) in an attempt to determine the longevity of their seeds. Since these trees are invading grazing lands in the southwestern United States such information would aid in determining management programs for areas from which junipers are removed.

The Forest Service's "Woody-Plant Seed Manual"[2] reports the limited information available on the germination and longevity of seeds of these trees. Utah juniper seeds have impermeable seed coats and dormant embryos. Many seeds of one-seed juniper have impermeable seed coats and dormant embryos. Some alligator juniper seeds have dormant embryos. Limited tests showed that one-seed juniper has 4- to 70-percent germination, and that alligator juniper has a 45-percent germination. Information on seed longevity is limited to alligator juniper for which germination of seeds stored in an unheated warehouse for 5 years fell to 30 per cent.

All seeds used in the present study were collected in Arizona under various circumstances. In 1956 seeds were collected in the field. All other seeds were obtained from either the Plant Materials Center of the University of Arizona at Tucson or the Rocky Mountain Forest and Range Experiment Station at Flagstaff. The storage history of seeds not collected personally was unknown; only the date and location had been recorded for the samples which were kept dry in bags or jars.

Sound seeds from each collection were soaked 48 hours in several changes of water and then planted ¼ to ½ inch deep in loam soil in wooden flats on June 24, 1957. These flats were placed in the greenhouse and kept moist. The

[1] Cooperative investigations of the Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, and the U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Flagstaff, Arizona.

[2] Forest Service. 1944. Woody-plant seed manual. U. S. Dept. Agr. Misc. Pub. 654. U. S. Govt. Printing Off., Washington, D. C.

numbers of healthy seedlings that emerged from the soil were recorded until the study was closed on March 31, 1958.

All samples tested had germinating seeds (Table 1).

TABLE I. Germination percentage of various-age juniper seeds planted in loam soil in the greenhouse on June 24, 1957

Year of Collection	PERCENT GERMINATION[1]		
	Alligator Juniper	One-seed Juniper	Utah Juniper
1956	30	61	49
1952	..	66	..
1948	16	46	25
1939	..	58	23
1936	..	54	..
1912	..	..	17

[1] Based on three subsamples of 50 seeds each except for the 1948 alligator and the 1912 Utah juniper collections, which consisted of single samples of 50 and 60 seeds, respectively.

Even the oldest seeds, 45-year-old Utah juniper, had 17-percent germination; 21-year-old one-seed juniper seeds had 54-percent germination; and 9-year-old alligator juniper seeds had 16-percent germination. No sound ungerminated seeds were recovered from the soil. Conclusions concerning relative seed survival cannot be made since factors other than seed age are confounded in the study.

These data show that seeds of these three junipers can survive extended periods of dry storage, probably because of the reported impermeable seed coats and dormant embryos of the seeds. Although storage conditions are not comparable with field conditions one might assume from these data that juniper seeds would be relatively unaffected by drought following seed dispersal. The seeds could lie in the soil through extended droughts and still be able to germinate when conditions became more favorable, thus facilitating the reproduction of juniper woodlands and possibly aiding reinvasion of ranges from which the junipers have been removed.

SUMMARY

1. Various-age seeds of alligator, one-seed, and Utah juniper that had been collected in Arizona and stored dry were tested in the greenhouse for germination percentage in loam soil during 1957-58.

2. All of the samples tested contained seeds that germinated.

3. The 45-year-old Utah juniper seeds had 17-percent germination; 21-year-old one-seed juniper seeds had 54-percent germination; and 9-year-old alligator juniper seeds had 16-percent germination.

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THE CONCEPT *VEGETATION* AND THE COMFORTABLE ECOLOGIST

The resolution of an apparent disagreement on the nature of plant ecology (McMillan, 1956, The status of plant ecology and plant geography, and Major, 1958, Plant ecology as a branch of botany) lies in the analysis of the concept *vegetation*. Because of the varied usage of the same word "vegetation," the scope of plant ecology and the organization of knowledge by McMillan and Major differ.

The viewpoints of Major and McMillan are different primarily with regard to the number of plants which are involved in the concept *vegetation*. Major has concluded that vegetation is composed of "associations of plants." McMillan, in dealing with all situations in which plants can occur, places the number of plants and the size of the area as variables, the extremes being one plant in a given area and many plants in a given area.

The inherent difficulties in determining the number of plants involved in the concept *vegetation* can be resolved in one of two ways. On the one hand, a definition of "two or more plants growing together in a given area" places one plant occurrences as non-vegetation. In the same way, the "many-plant" definition of Major places one, two, three, etc. plant occurrences as non-vegetation. Any arbitrary definition of more-than-a-particular-number will exclude all other situations. The usage of the word "vegetation" accompanied by a definition can offer one resolution of seeming disagreements. On the other hand, if a class *vegetation* is set up in a propositional form as the "sum total of plant life in a given area," the number of plant-members becomes a variable. In this latter proposal, all situations in which plants can occur, actually or theoretically, are included. If the concept *vegetation* is accepted in this latter form, it will include the various numerically-determined classes, many-plants, two-or-more, associations-of-plants, etc.

The most inclusive usage of the concept *vegetation* will be that in which the number of plants and the size of the area are variables. In a highly inclusive sense, the vegetation of the earth can be discussed. In more restricted application, the vegetation of a greenhouse is recognized as is the vegetation of a test-tube. The potted plant and its associated microflora become the vegetation of the pot habitat.

Unlikely as it may seem, one pollen grain in a room can constitute the vegetation of that region if it represents the "sum total of plant life of that given area." While this is an extreme situation that would require rather special conditions to set up and to measure, it demonstrates the application of the concept *vegetation* to the isolated individual.

Although Major understood the usage of "community" by McMillan to be in a non-plant sense, apparently because of nomenclature (Lincoln community, Halsey community, etc.), McMillan intended a position in a vegetational hierarchy. This hierarchy would utilize the concept *community* for one or more populations in a common spatial arrangement. In its simplest form, a community could consist of one population of one individual. In the example above, the pollen grain, as an individual microgametophyte, would represent a population and a

community in the vegetational hierarchy. The concept *population* would deal with one or more individuals of a close genetic lineage in a common spatial arrangement. In most cases, a population has more than one member and usually these are referable to one species. In the example above, the inclusion of only one individual within the spatial arrangement creates a population of one. The individual upon which the hierarchy is based owes its identity to a distinct physiology and a distinct morphology which are expressions of its genetic potential under a given set of environmental conditions.

In broad scope a vegetational science would include all approaches to the understanding of vegetation. The separation of floristic botany from vegetation science as proposed by Egler (1942) and recently by Major (1958) would find no distinct line of departure. Vegetation science should include basic distributional studies (referred to as plant geography, McMillan 1956), as well as those which deal with all individuals and with problems relative to the position of these individuals in any arrangement and in any particular habitat (referred to as plant ecology, McMillan, 1956). The separation of ecology into autecology and synecology finds no logical basis in the concept *vegetation* as applied to one or more plants and to their occurrence in populations of any size, configuration, and breeding structure, and to their occurrence in communities of any size, configuration, and combination of one or more populations.

As vegetation scientists, Major and McMillan, as well as others, seek a level of ecological comfort that is most fitting their background, needs, and interests. As expected, the range of ecological comfort is great and will vary among the kinds of vegetation offering a satisfactory object of study. Just as some workers find comfort in natural vegetation, others find solace in weedy or introduced plant life. Some are at ease only with vegetation in the field, and some freely introduce vegetation to laboratory analysis. Just as there are comfortable positions in grassland, equally available positions occur in forests, in crops and in greenhouses. The problems of vegetation can be studied profitably from any comfortable position.

Among vegetation scientists, there are those whose interest is primarily in plotting distribution and there are those whose interest is primarily in understanding the nature of the distributions. And as we all know, an interest-spectrum provides a broad continuum between these extremes. Near the one extreme will be the vegetational photographer and near the other will be the vegetation scientist who uses as many tools as possible to further our understanding of vegetation.

The region of comfort among those who brave the label of "ecologist" is dictated in part by teaching and/or research. The comfortable ecologist who finds time only for teaching may be at ease within a system of ecology. For such purposes, he may choose the Clementsian system or the Braun-Blanquet system or any other which is relatively complete within itself. If an ecologist has a limited amount of time for research, he may remain comfortable within a particular system. Each system usually provides patterns for research and these patterns have been tested and have produced sound basic data. Within most systems, the concepts are based upon the recognition of species and the concentration is usually upon the distributional status of particular combinations of species.

Many comfortable ecologists are primarily interested in soils and/or climates and find that correlations with plant distributions, of single species or of combinations of species, are a profitable and basic venture. Major objects to labelling these endeavors as correlative geography partially on the grounds that geography specifically deals with "landscapes or regions." Hartshorne (1958) has evaluated at length the various viewpoints and usages within the concept *geography* and concludes that geography maintains a defensible position among the sciences as one of the chorographic studies. Apparently the geographer is not bound by the complete rigidity suggested by Major in the separation of geography and chorology. Nor are all geographic studies restricted to the study of "landscapes or regions," terms upon which geographers find no common agreement. Hartshorne (1958) suggests that "geography has no one particular category of objects or phenomena as its specific subject of study but studies the multitude of heterogenous things as integrated in space."

There are comfortable ecologists who use varying mixtures of physiology, morphology, and genetics, to seek further understanding of the distributional patterns within vegetation. In evaluating individual, population, and community relationships, they are seeking an understanding of the harmony of vegetation and habitat.

Still other ecologists are comfortable in vegetational theory. Their contributions through semantical and logical analyses will prove a service to all whose comfort-range places them in a position to compare systems. Much ecological disagreement can be resolved through logical analyses and from such contributions can come, among other things, a foundation for understanding the basis for the broad range of comfort and interests among ecologists.

Multitudes of comfortable ecologists are concerned with the economic application of the principles of plant distribution in forestry, range management, pasture management, horticulture, and agronomy, among others. The reliance of the applied aspects upon the fundamental concepts makes it further necessary that ecological systems be compared and semantically cleansed.

In conclusion, the problems of vegetation might be likened to those involving an object of study within a sphere with many tiny openings. In trying to study the concealed object, previous investigators devised magnifying tubes for peering into the sphere. Through these tubes, which might be called vegescopes, the object of study can be observed. If we choose the Clements vegescope, we will get a view of the object. If we look through the Braun-Blanquet vegescope, we will get another view. If we compare the two views, both offer an orderly arrangement of the object of study and both offer a terminology for discussing the contents. The Gleason view displays raw distributional data, less order, and provides less built-in satisfaction. If the ecological comfort-quotient allows further viewpoints, there are many available vegescopes. Often the view is different because of the angle of the vegescope or because of a particular lens arrangement in the vegescope. Again and again we would have to remind ourselves that basically the vegescopes were directed at the same confined object. If our comfort-range allows, we can look through vegescopes that have been manufactured by workers, labelled non-ecologists, the physiologists, the morphologists, the geneticists. Through their vegescopes the individual components of the vegetation are under higher magnification. Through the physiological vegescope the individuals are observed as they are functionally affected by the habitat. The genetic vegescope displays the nature of variation among individuals. The morphological vege-

scope shows the modification of structure under different habitat pressures. We may even have to wait in line occasionally when we find taxonomists peering down the same vegescopes.

The realm and status of ecology will undoubtedly furnish material for many articles beyond those chiefly under consideration. The suggestion is offered that an ecological system be sufficiently broad with relatively simple, even obvious, divisions for the inclusion of all who are interested in vegetation in the broad sense. Since the fundamental goal is the further understanding of the vegetational hierarchy, we are apt to need potential sites for new approches rather than reject them as not a part of vegetation science.

References

Egler, F. E. 1942. Vegetation as an object of study. Philosophy of Science **9**: 245-260.

Hartshorne, R. 1958. The concept of geography as a science of space, from Kant and Humboldt to Hettner. Annals Assoc. Amer. Geog. **48**: 97-108.

Major, J. 1958. Plant ecology as a branch of botany. Ecology **39**: 352-363.

McMillan, C. 1956. The status of plant ecology and plant geography. Ecology **37**: 600-602.

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TEMPERATURE CHANGES WITHIN CYPRESS LOGS IN THE KENYA HIGHLANDS

Introduction

In nearly all branches of field research work, climate enters as one of the controlling factors, to a lesser or greater degree. The difficulty that confronts the investigator in the tropics is that, in general, the meteorologist will not be able to give a very good idea of the climate of the zone in which the investigator is interested owing to lack of observations. Especially is this true in the application of climatology to agriculture and forestry, for here the researcher usually needs details of the micro-climate of his area, information which is seldom available.

This series of observations was carried out to investigate the possibility that the larvae of the Cerambycid borer, *Oemida gahani* Dist., could be killed by the temperature increase near the centre of cypress logs exposed to the sun, in the heartwood of which they normally bore. It had been noticed when examining recently felled logs in plantations, that some larvae had died and were in a flaccid condition which, it was thought, could have resulted from partial dehydration due to the increase in temperature and drying out of the exposed logs. Such larvae were generally found near the outer edge of the heartwood, about 4 in. to 6 in. from the long surface, from which the bark had not been removed. It was therefore decided to measure the temperature changes near the centre and surface of cypress logs, similar in size to those in which the dead larvae had been found, under clear sunny conditions in which the maximum effect could be produced. Temperature changes in logs with bark removed and also in dry seasoned logs were measured for comparison. Some observations of the effect of different temperatures on Oemida larvae and their resulting survival times, were carried out by exposing logs, in which larvae were boring, to increasing temperatures in an electric oven. The logs were *Cupressus lusitanica* Mill.

Observations

The first observation was made using two seasoned logs about one foot long and 8 in. diameter, one with the bark removed, the other with the bark on. Two thermometers were inserted longitudinally into each log to a depth of 4 in., one about ½ in. below the surface, the second about 4 in. below. The preliminary test showed that after one hour's exposure to sunshine at ground level (7000′) at 17.20 hrs, the temperatures were:

Bark-on log	—½″—123° F	4″—94° F
Bark-off log	—½″—106° F	4″—89° F

The next test was to place the logs in the sun and to take the readings every ten minutes. The pattern of temperature is given in Fig. I. This shows the marked gradients, of the order of 20 F°/1 in. that can exist in both logs after prolonged exposure to sun.

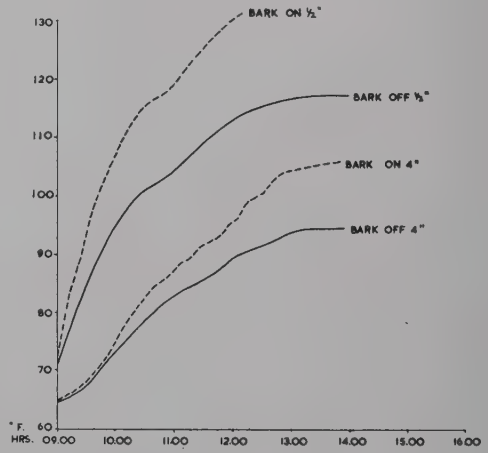

Fig. 1. Dry logs in sun.

It was decided that the rate of cooling should be studied and as the natural climatic conditions were unsatisfactory, recourse was made to a constant temperature room. The logs were left in the room overnight and upon removal the next morning both recorded 103° F at ½ in. and 101° F at 4 in. They were then placed in a room at a temperature of about 68°F. The cooling is almost identical in both logs but, as would be expected, the core cools less rapidly than the perimeter (Fig. 2).

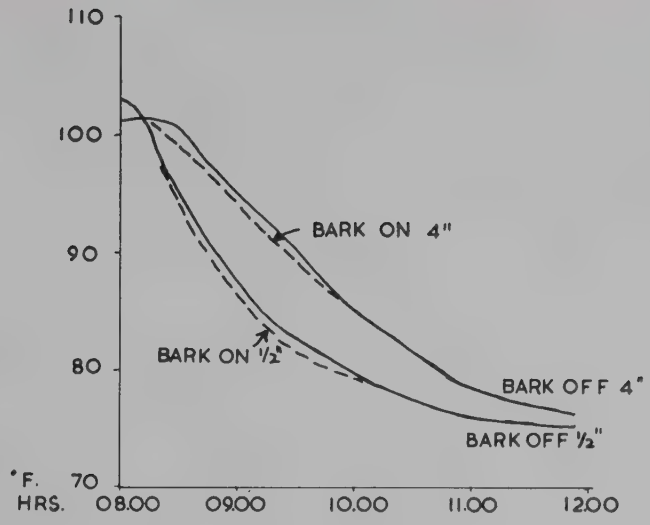

Fig. 2. Cooling Curve.

The next experiment was similar to the first but now two green pieces of cypress were used. Readings were taken at ten minute intervals and plotted in Fig. 3. It

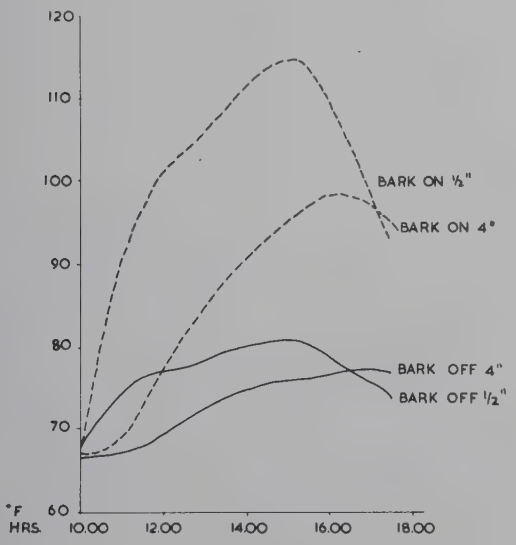

Fig. 3. Fresh wet logs in sun.

is immediately noticeable how much lower the temperatures now are, about 20° F near the surface of the barked log, thus showing how evapotranspiration is successful in lowering the wood temperature. During a similar period the logs were exposed outside, but now shaded from direct sunlight. The temperatures followed an identical trend but with a very greatly reduced amplitude, reaching maxima of 77.8° F (bark-on) and 69.0° F (bark-off).

The final experiment was to expose four pieces simultaneously, firstly in the shade, then in the sun. The same relative values as before were obtained. Under shaded conditions the only significant difference was for the fresh bark-off log which had a maximum some 10° F below the other three. In the sun, the dry bark-on log again exceeded 130° F, while the fresh bark-on log reached 115.8° F. The highest temperature recorded at the ½ in. depth in the green bark-off log was 83° F, less than 10° F higher than the air maximum. The inner temperature reached a maximum at about 16.30 hours when the bark was left on, but with bark removed this was reached at about 16.00 hrs.

To investigate the effect of temperatures, at and above those reached in these experiments, on Oemida larvae, a number of larvae, boring near the centre of fresh and seasoned cypress logs and thus similarly situated to the deep thermometers, was exposed to these temperatures in an electric oven. They were found to survive from 6½ to 16½ hours at 135° F in fresh, unseasoned logs and for 5½ hours at from 122° F to 131° F in seasoned logs.

Summary and Conclusions

Temperature measurements were taken within seasoned and freshly felled cypress logs under various conditions. These showed that seasoned timber reached much higher temperatures than green wood, values of well over 130° F being recorded. The thermal gradient within the logs was very steep.

Exposure of Oemida larvae boring near the centre of similar logs, to comparable temperatures in an electric oven, showed that they could survive at higher temperatures, sustained for longer periods, than those measured in field conditions. As the highest temperatures measured in the field occurred only near the surface of the seasoned log, it is considered unlikely that Oemida larvae, boring in the heartwood of both fresh and seasoned cypress logs, could be killed by the increase in the temperature of the timber, resulting from its exposure to the sun in plantations.

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ON THE USE OF MATHEMATICAL NOTATION IN ECOLOGICAL LITERATURE

This note is a plea for the increased use of mathematical notation where appropriate in ecological literature. Provided it is used with care, mathematical notation offers to authors, readers, researchers, and editors the following distinct advantages: (1) substantial saving of premium page space with attendant increase in the flow of material through editorial offices, (2) precision communication of logical thought frequently beyond the capabilities of the written word, (3) increased assurance of reproducibility of methods and results by those applying the techniques of others, and (4) increased speed and precision in translation to languages other than the original. It is worth repeating, however, that these advantages accrue in proportion to the care used by the author in the use of the notation.

The use of mathematical notation in itself does not assure the validity of the thoughts or concepts being expressed by the notation, but by the same token it frequently offers the above advantages even to non-mathematical thinkers and authors. In other words, I believe the excuse ". . . but I'm no mathematician" need not prevent the use of mathematical notation on the part of technical writers or the comprehension of it by the reader who is more than casually interested in the material being presented.

As an example of a case in which mathematical notation may serve even though mathematical manipulation is not involved, consider the following definition of an hypothetical index to be derived from field data on measurements of various quantitative characters of vegetation.

The value of the Index, I, for the i-th of n species is

$$I_i = \frac{1}{3}\left[\frac{A_i}{\sum_{i=1}^{n} A_i} + \frac{B_i}{\sum_{i=1}^{n} B_i} + \frac{C_i}{\sum_{i=1}^{n} C_i}\right]; i = 1,2,3,\ldots,n$$

where A_i = value of the character A for the i-th species
B_i = value of the character B for the i-th species
and C_i = value of the character C for the i-th species.

This tells the reader exactly what the author has in mind and how to calculate the index. It does not tell him how to make his measurements in the field, nor does it tell him how to interpret the value of I derived. Notice that the validity of the concept being expressed is not laid open to question by the fact that mathematical notation is used. The author is simply stating concisely the definition of an index number. If the use and interpretation of the index are open to question, they would be so even if words had been used to express it. In short, *mathematics,* in the extended sense, is not involved here but only *mathematical notation* as a sort of precision shorthand. In this case advantages 1, 3, and 4, but not 2, are realized.

As a case in which advantage 2—communication of logical thought—may be realized, consider the following abbreviated excerpt from the literature (Lowry 1956: 424):

"Let us assume the following equation is correct:

$$dW/dt = A(E_s - E) \qquad (4)$$

Since the relative humidity is defined as the ratio $r = E/E_s$, we may rewrite equation (4) as

$$dW/dt = A(1 - r)E_s$$

and if we define $R = (1 - r)$, we have

$$dW/dt = ARE_s.$$"

The reader can imagine trying to communicate these manipulations entirely in words. Notice, however, that in this case the original assumption of equation (4) may be, and in fact has been, quite open to question. Though the manipulations are legitimate, the use of mathematical notation has not assured the validity of the ideas expressed.

My readings in the ecological literature, limited though they may be, have convinced me that far too often an author's ideas have been rendered fuzzy, space has been literally wasted, and complex logical thought has not been reliably communicated because of an avoidance, for whatever reason, of the use of mathematics and mathematical notation. Hence the present note.

Reference

Lowry, W. P. 1956. Evaporation from forest soils near Donner Summit, California, and a proposed field method for estimating evaporation. Ecology **37**: 419-430.

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SOILS AND FOREST GROWTH ON DIFFERENT ASPECTS IN THE TANANA WATERSHED OF INTERIOR ALASKA[1]

One of the frequently encountered characteristics of the boreal landscape is the extremely abrupt demarcation of soil-vegetation types.

Sharp differentiation of plant communities may be caused by a number of conditions, such as severe fires, irregularities in drainage, invasion of mosses, particularly Sphagnum, sporadic occurrence of permafrost, and solifluction. However, none of these alterations of the vegetative cover is comparable to the radical and lasting changes imposed by micro-climatic influences on slopes of different exposures, especially those of northern and southern aspects.

The effect of topographic features on the occurrence of permafrost, soil drainage, and distribution of vegetation in the Tanana Valley has been noted by several investigators (Bennett and Rice 1919; Péwé 1954; Hopkins et al 1955; Lutz and Caporaso 1958). In view of the practical importance of this relationship, it seemed desirable to record the observed variation in soil and vegetative cover by appropriate quantitative analyses.

One area which reflects in a conspicuous manner the soil-forming and ecological influences of topography is

[1] Joint contribution, Alaska Agricultural Experiment Station and Soil Conservation Service, U. S. Dept. Agr.

TABLE I. Content of nutrients and associated fertility factors in a profile of Gilmore silt loam on southern slope of ridge

Horizon	Depth of Sample (inches)	Reaction (pH)	Tot. N (pct.)	Tot. C (pct.)	C/N ratio	Avail. P_2O_5 (p.p.m.)	Avail. K_2O (p.p.m.)	Exch. Ca (me./100g)	Exch. Mg (me./100g)
$F(A_{01})$	3-1	6.3	1.41	34.10	24.2	380.0	1,900	102.2	13.4
$H(A_{02})$	1-0	6.0	0.80	20.60	25.7	128.5	618	56.6	8.9
A_1	0-2	5.5	0.12	2.24	18.5	87.6	102	8.0	3.6
$A_2(?)$	2-5	5.2	0.04	0.70	17.5	6.6	64	2.8	3.5
B_2	5-8	5.2	0.04	0.61	15.0	4.6	60	3.5	3.9
	8-8¼	5.0	0.06	1.00	16.6	5.1	120	5.2	6.7
B_3	8¼-17	5.2	0.04	0.41	10.2	11.3	47	3.5	4.9
D	17+	6.1	0.03	0.14	4.7	1.8	38	3.1	3.8

located in the Rosa Creek Forest Reserve, about 12 miles southwest of the village of Ester. This area, unlike most of the Fairbanks region, has not been burned or logged for at least one hundred and thirty years. The recently constructed Fairbanks-Nenana road, which traverses the Reserve along a high narrow ridge, provided access to the object of this study—steep southern and northern slopes with gradients of approximately 35 per cent on either side of this road at an elevation of about 1,300 feet.

Both of these slopes are covered with a mantle of micaceous loess, which rests on shattered and folded Birch Creek schist, the country rock. On the southern slope, a well drained soil of the Subarctic Brown Forest group (Kellogg and Nygard 1951), Gilmore silt loam, has developed. This soil supports mature white spruce (*Picea glauca* var. *glauca*) which should be rated among the most rapidly growing and valuable forest stands of interior Alaska. On the northern slope, however, a poorly drained "highmoor" Half-Bog soil is occupied by a stand of non-merchantable dwarfed black spruce with an extremely slow growth rate (Fig. 1).

FIG. 1. Forest cover on a topographical complex in the Rosa Creek Forest Reserve, Alaska, at an approximate elevation of 1,300 feet. At left, a southern slope shows white spruce, 110 to 130 years old, of a high site index, and with yield approaching 15 Mbf per acre; at right, a northern slope shows black spruce, 115 to 130 years old, averaging 3.5 cords per acre.

Descriptions of soils and forest conditions observed on these two aspects, and the results of soil, floristic, and mensuration analyses follow.

Southern Exposure. The following profile of Gilmore silt loam was observed on the southern slope about 100 yards below the crest of the ridge.

S	4½-3″	Live *Hylocomium* mosses.
$F(A_0')$	3-1″	Very dark brown (10 YR 2/2)[1] partly decomposed matted plant remains, mostly of mosses. Many roots and fungus mycelia. (Fermentation layer of mycelial moss mor).
$H(A_0'')$	1-0″	Very dark brown (10 YR 2/2) spongy organic matter in advanced stages of decomposition, with few mycelia and high concentration of roots. Abrupt smooth lower boundary (Humified layer of mycelial moss mor).
A_1	0-2″	Very dark grayish brown (10YR 3/2) micaceous silt loam. Very weak fine platy structure, crushing easily to weak very fine granules. Very friable. Roots plentiful. Clear smooth boundary.
$A_2(?)$	2-5″	Brown (10YR 5/3) micaceous silt loam. Weak very fine platy structure. Very friable. Roots plentiful. Few angular schist pebbles in this and lower horizons. Clear wavy boundary.
B_2	5-8″	Dark brown (10YR 4/3) micaceous silt loam. Moderate very fine platy structure. Very friable. Roots plentiful. Lowest ½″ is somewhat lighter in color. Abrupt wavy boundary.
	8-8¼″	Thin band, roughly horizontal, of dark brown (10YR 3/3) heavy silt loam. Moderate fine subangular blocky structure, with faint clay skins on peds. Friable. Abrupt wavy boundary.
B_3	8¼-17″	Dark grayish brown (10YR 4/2) micaceous silt loam. Moderate very fine platy structure. Very friable. Few roots. Very thin irregular band of heavy silt loam in middle or horizon. Abrupt wavy boundary.

[1] Munsell color notation for moist soil.

TABLE II. Content of nutrients and associated fertility factors in a profile of Ester silt loam on northern slope of ridge

Horizon	Depth of Sample (inches)	Reaction (pH)	Tot. N (pct.)	Tot. C (pct.)	C/N ratio	Avail. P_2O_5 (p.p.m.)	Avail. K_2O (p.p.m.)	Exch. Ca (me./100g	Exch. Mg (me./100g)
F(A_0)	10- 0	4.0	0.51	32.1	62.9	82.6	397	8.2	8.3
A_1	0- 4	4.5	1.02	28.2	27.7	58.0	69	9.5	2.7
G	4-10	5.1	0.46	11.5	25.0	30.9	75	5.2	1.5

D 17+ Weathered micaceous schist.

The results of analyses of this profile are incorporated in Table I. Strongly acid reactions and an adequate well balanced supply of nutrients in the entire profile are outstanding characteristics of this soil.

The forest cover consists principally of white spruce, 110 to 130 years old. The dominant trees are 10 to 14 inches in diameter, and 79 to 91 feet high. The stand has a slight admixture of trembling aspen and a sparse understory of highbush cranberry, *Viburnum edule* (Michx) Raf., and Sitka alder, *Alnus sinuata* (Reg) Rydb. The yield at 70 per cent stocking approaches 15 Mbf. per acre.

The ground cover is made up of a solid carpet of *Hylocomium splendens* (Hedw) and *Pleurozium schreberi* (Brid.) Mitt. mosses with a rare occurrence of *Mertensia paniculata* (Ait.) G. Don, *Pyrola secunda* (L.), and semi-parasitic *Geocaulon lividum* (Richards.) Fern. The scarcity of vascular plants in the ground cover, as well as the lack of natural reproduction of spruce, is the outstanding feature of this forest type.

The stand of white spruce extends to the summit of the ridge where it encounters in a "head-on" fashion the stand of black spruce on the north slope, so that the

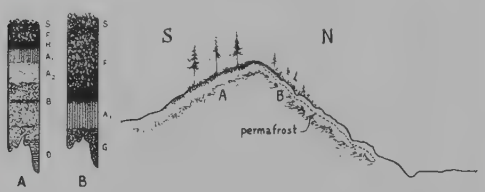

FIG. 2. Schematic cross-section indicating nature of soils and forest cover on southern (A) and northern (B) slopes in the Tanana watershed.

tension zone between the two types does not exceed a few yards (Fig. 2).

Northern exposure. The profile of Ester silt loam[2] described below was observed on the northern slope of the ridge, about 100 yards below the summit.

S 13-10″ Live *Sphagnum* mosses.

F(A_0) 10-0″ Peat-like layer of Sphagnum mosses, only slightly decomposed; penetrated by a few mycelia and many roots.

A_1 0-4″ Very dark grayish brown (2.5Y 3/2) micaceous silt loam with lenses and pockets of black (N 2/0) amorphous organic matter. Few roots. Frozen in the lower part (Sept. 20, 1958), but in spite of this containing *Enchytraeidae*, light colored "ice worms," and unidentified beetles resembling in size and appearance *Ips lineatus*.

G 4-10+ Olive gray (5Y 4/2) micaceous silt loam with distinct olive brown mottling and black and dark brown streaks. Few to no roots. Frozen. Depth to the underlying schist substratum is approximately 18 inches.

[2] Uncorrelated series.

Analyses of this profile are reported in Table II. Extreme acidity, high C/N ratios and low exchangeable calcium in the F horizon are adverse fertility factors of this soil. The difference in thickness of organic layers in soils developed on southern and northern exposures is illustrated in Figure 3.

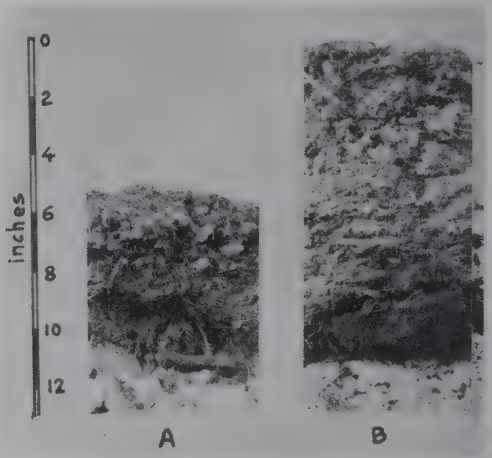

FIG. 3. Thickness of surface organic layers in soils developed on southern (A) and northern (B) slopes.

The forest cover on this soil is made up mostly of black spruce 115 to 130 years old. The average diameter of the trees is 2.9 inches; height of the tallest trees averages 23 feet. The volume at 50% density is between 3 and 4 cords per acre. The stand is accompanied by scattered Sitka alder (*Alnus sinuata*, Reg., Tydb.), bog birch (*Betula glandulosa*, Michx.), willows (mostly *Salix glauca*, L.), and spirea (*Spirea beauverdiana*, Schneid.)

The composition of the ground cover is expressed by means of D/F quotients, where D is the number of plants of a species encountered per 100 feet of a linear transect, and F is the frequency of occurrence of these plants in percent of 10 foot linear segments. The surface layer consists predominantly of *Sphagnum* spp., including *S. girgensohnii* Russ., *S. capillaceum* Schimp., and *S. fuscum* (Schimp.) Klinggr., and occasional patches of *Polytrichum commune* Hedw. and *P. strictum* Brid. The moss cover is dotted with lichens, *Cladonia sylvatica* (L.) Hoffm., *Cladonia rangiferina* (L.) Web., *Cetraria islandica* (L.) Ach., and *Peltigera aphthosa* (L.) Willd. The association of vascular plants is made up of *Vaccinium Vitis-Idaea* L. (241/100), *Vaccinium uliginosum* L. (13/20), *Ledum decumbens* (Ait.) Hult. with some *L. palustre* L. (74/100), *Rubus chamaemorus* L. (40/85), and *Eriophorum vaginatum* L. (12/25).

From the above, it is obvious that in the subarctic region a distance of a few dozen yards between slopes of cardinal orientation can result in radical changes in the genetic nature of the soil, the vegetative cover, and the entire pattern of silvicultural management and land utilization.

The southern slope now supports a forest stand which "cries" for the removal of some of the mature timber to permit more light and precipitation to reach the ground, and for the breaking by scarifying skidding of the insulating and contraceptive layer of mosses. These measures are imperative for an acceleration of the retarded increment and the establishment of unduly delayed natural reproduction. Under intensive forest management, an artificially established plantation of elite stock, set in contour-plowed furrows, could produce a double or even a triple increment in comparison with volunteer forest cover. Should population pressure ever demand an expanded farming program, Subarctic Brown Forest soils on southern slopes of moderate gradient could produce high protein forage, comparable or even exceeding in nutrient value that of the temperate zone.

The northern slope with its soil and forest cover is outside of the domain of either silviculturist or agronomist, for this ecological unit would not provide even a small return on invested labor. At the same time, these Half-Bog soils are not synonymous with unproductive land. They provide food and habitat for many members of the wildlife, an important item in the regional economy. If and when Alaska is ready to compete with Scandinavia in the production of canned fruits, these soils could provide abundant crops of lingonberries, bilberries, and cloudberries of superb flavor. Light broadcast applications of a complete, readily soluble fertilizer would appreciably increase the yield and nutrient value of the crop, thus making feasible the use of efficient harvest methods.

References

Bennett, H. H. and Rice, T. D. 1919. Soil reconnaissance in Alaska with an estimate of the agricultural possibilities. USDA Bur. of Soils, Washington, D. C., Field Operations, 1914.

Hopkins, D. M., Karlstrom, T. N. V., and others. 1955. Permafrost and ground water in Alaska. U. S. Geol. Surv. Prof. Paper 264-F, Washington, D. C.

Kellogg, C. E. and Nygard, I. J. 1951. Exploratory study of the principal soil groups of Alaska. U. S. Dept. Agr. Monograph 7.

Lutz, H. J. and Caporaso, A. P. 1958. Indicators of forest land classes in air-photo interpretation of the Alaska interior. Alaska Forest Research Center, Juneau. Station Paper 10.

Péwé, T. L. 1954. Effect of permafrost on cultivated fields, Fairbanks Area, Alaska. U. S. Geol. Surv. Bul. 989-F.

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THE RELATION BETWEEN CROWDING AND WEIGHT OF ADRENAL GLANDS IN CHICKENS[1]

Introduction

In an attempt to achieve greater labor efficiency and reduce housing costs, poultrymen have tended to increase the number of birds per given area. However, little or no attention has been paid to the effects of such intensification on the avian physiology. This study was undertaken to examine relative differences in weight and histological appearance of adrenal, thyroid and pituitary glands of laying chickens held at two different population densities. Total adrenal cholesterol was also determined since depletion is considered an index of corticosteroid output (Rosenfeld 1955).

Increased activity of the pituitary-adrenal cortex axis, as manifested by adrenal hypertrophy, was originally advanced by Selye (1937) as part of the animal's systemic response to non-specific stress. The response of young chickens to various stressors was studied by Garren and Schaffner (1952, 1954, 1956) who found that musuclar fatigue, exposure to cold, and simulated high altitude caused adrenal hypertrophy and atrophy of the thymus and bursa of Fabricius. According to Garren and Barber (1955) adrenal enlargement and bursa involution accompanied the usual symtoms of the disease when young New Hampshire and Rhode Island Red chickens were inoculated with Fowl Typhoid. Histological study revealed that the hypertorphy was in the interrenal (cortical) sections of the gland.

The possibility that population density might constitute physiological stress has been studied in mammals. A significant relationship between adrenal weights relative to body length and population density was obtained by Christian and Davis (1956) in 49 samples of urban Norway rats. Louch (1956), studying 3 confined populations of meadow voles, noted that greater adrenal activity accompanied higher population density.

Materials and Methods

On November 1, 1952, 400 6-month old Single Comb White Leghorn females from the regular Pennsylvania Agricultural Experiment Station stock were randomly

[1] Authorized for publication on April 23, 1958, as paper No. 2251 in the journal series of the Pennsylvania Agricultural Experiment Station.

divided into 4 groups: 2 groups of 150 birds each and 2 of 50 each. The groups were housed in 4, 10′ x 20′ pens in a long poultry house so that the initial floor space allowance for the 150 bird groups was 1.33 square feet per bird and for the 50 bird groups 4.000 square feet per bird, The pens were designated as A, B, C, and D consecutively, with groups at 1.33 square feet occupying pens A and D and those at 4.00 square feet occupying pens B and C. A solid partition separated pens A and B from pens C and D. Beginning 3 feet from the floor, 1″ x 4″ welded wire replaced the solid partitions between the A and B pens and between the C and D pens allowing diffusion of air between pens and helping to maintain similar temperatures in the unequally populated pens. Daily high and low temperatures were noted in each pen from Fisher Maximum-Minimum thermometers which were hung on a solid wall, 4 feet from the floor, equidistant from the front and rear.

Multiple-tiered roots and feeders which have been successfully utilized at the Pennsylvania State University poultry farm (Bressler and Jones 1957) were modified for use with all groups. An assembly consisting of 3 tiers of roosts, 2 roosts per tier, over a dropping pit was placed in each pen, providing 0.48 feet of roosting space per bird. Feeders were placed on each tier, between the roosts, so that linear feed space equaled roosting space. Water troughs, hung directly over the wire covered droppings pit, provided 0.16 linear feet per bird. A 100-watt incandescent lamp with reflector was in the center of the ceiling of each pen and was automatically controlled to allow 14 hours of light per day. The standard Pennsylvania Agricultural Station all-mash poultry breeder ration was fed *ad libitum*. All groups were maintained under the above conditions throughout the 5½ month experimental period with no attempt being made to replace the total of 7 individuals which died.

At the time of housing, 25 birds in each group were randomly selected and marked for identification. Beginning on April 14, 1957, from 2 to 8 birds of those originally identified were weighed, sacrificed by bleeding, and autopsied daily until 20 birds from each group had been taken. Fifteen days were required to complete the 80 bird sample. Adrenal, thyroid and pituitary glands were carefully dissected, cleaned, then weighed to the nearest 0.2 mg on a torsion balance. The first 3 sets of glands from each group were saved for histological examination. Immediately after weighing, the remaining sets of glands were placed in marked vials and quickly frozen. Total adrenal cholesterol was determined by the method of Knobil *et al.* (1954).

Means and standard errors of the means were calculated for the gland weights, the gland weights relative to body weights, and the total adrenal cholesterol of each group. The significance of the differences between density groups was calculated by analysis of variance. Regression coefficients (^{b}yx), standard error of ^{b}yx and the significance of ^{b}yx were calculated according to methods described by Snedecor (1954). All randomizations were achieved by means of tables of random numbers.

Results

Final live body weights, gland weights and gland weights relative to body weight are shown in Table I. Body weights, thyroid and pituitary weights of birds kept at different density levels did not differ significantly. However, the mean adrenal weights of those groups held at 1.33 square feet per bird were significantly greater than those held at 4.00 square feet ($P < 0.01$). The mean adrenal weights relative to body weight of the more densely populated groups were also shown to be significantly heavier ($P < 0.05$).

Examination of the data revealed that adrenal weights were apparently related to the day on which the bird was sacrificed. Consequently, data from pens of equal density were combined, and a simple regression equation calculated for both levels of population density (Figure 1). The regression coefficient ($^{b}yx = -1.9$) for the

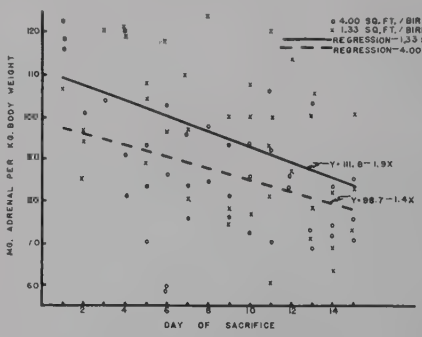
4.00 SQ. FT. / BIRD
1.33 SQ. FT. / BIRD
REGRESSION-1.33 SQ. FT. / BIRD
REGRESSION-4.00 SQ. FT. / BIRD
Y = 111.6 - 1.9X
Y = 98.7 - 1.4X
MG. ADRENAL PER KG. BODY WEIGHT
DAY OF SACRIFICE

Fig. 1. Effect of day of sacrifice on Relative adrenal weight. The plotted data are individual values: 1.33 square feet per bird (X); 4.00 square feet per bird (0).

groups held at 1.33 square feet per bird was highly significant ($P < 0.01$); the coefficient ($^{b}yx = -1.4$) for the groups held at 4.00 square feet per bird was significant

Table I. Final Body Weight, Adrenal, Thyroid and Pituitary Weights Results expressed as the means ± $Se_{\bar{x}}$

Group	Initial Floor Space	No. of Birds	Final Body Wt.	Adrenal** Wt.	Adrenal Wt./Kg.* Body Wt.	Thyroid Wt.	Thyroid Wt./Kg. Body Wt.	Pituitary Wt.	Pituitary Wt./Kg. Body Wt.
	sq. ft. /bird		gm.	mg.	mg.	mg.	mg.	mg.	mg.
A	1.33	20	2175.5±64.6	206.2±6.0	97.0±3.7	179.4±12.0	83.7±5.2	11.5±0.4	5.4±0.2
D	1.33	20	2295.0±69.2	209.3±8.2	92.3±3.9	196.4±11.6	86.0±5.3	11.9±0.5	5.3±0.1
B	4.00	20	2115.0±63.3	183.9±6.3	88.1±3.5	185.9±11.8	88.1±4.9	11.4±0.5	5.5±0.3
C	4.00	20	2192.5±66.1	185.3±5.9	85.6±3.3	178.4±11.1	82.4±5.1	11.3±0.4	5.2±0.1

* Difference between floor space levels significant ($P<0.05$).
** Difference between floor space levels highly significant ($P<0.01$).

($P < 0.02$). This indicated that adrenal weights in both floor space groups were significantly related to the day of sacrifice and that, within the range of these data, adrenal glands weighed progressively less as autopsies continued through the 15 day period. The slopes of the regression lines did not differ significantly.

TABLE II. Total Adrenal Cholesterol Results expressed as means $\pm$ $Se_{\bar{x}}$

Group	Initial Floor Space	No. of Determinations	Total Adrenal Cholesterol
	sq. ft./bird		g./mg. adrenal
A	1.33	16	24.37±2.14
D	1.33	17	24.93±1.68
B	4.00	15	30.22±1.86
C	4.00	16	25.07±1.70

Total adrenal cholesterol was determined as μg of cholesterol per mg. of adrenal (Table II). The difference between floor space groups was not statistically significant. Microscopic examination of histological samples revealed adrenal cortical area hypertrophy apparently due to hyperplasia in these areas. However, individual cells showed no apparent abnormalities.

DISCUSSION

The adrenal, thyroid and pituitary weights shown in Table I are within the range of data reported for adult female chickens by Latimer (1924) and Juhn and Mitchell (1929). However, the significantly heavier adrenals of birds held at 1.33 square feet per bird compared to those held at 4.00 square feet per bird suggest that the conditions of over-population described had produced an increase in adrenal cortical activity. Histological observations indicate that increased population density acted only as a mild exogenous stressor, probably well within the birds' adaptive ability. The adrenal cortical area hypertrophy generally observed in birds from the more densely populated groups was in the form of a mild cellular hyperplasia. In no individual was there an indication of the acute hyptertrophy of the cells or lipoidal depletion observed by Garren and Barber (1955) in chickens subjected to the extreme endogenous stress of disease. The total adrenal cholesterol data in Table II are in accord with the postulate that the population stress imposed was subacute in nature. Although cholesterol values tended to be lower in more densely populated groups, the difference was not significant. If cholesterol depletion is considered an index of adrenal corticoid secretion, it would appear that such secretion was not materially increased.

Relative adrenal weights were significantly related to the day on which the chicken was sacrificed. Daily declines in adrenal weight of 1.9 and 1.4 mg per kg body weight were observed in the 1.33 and 4.00 square foot groups respectively as the 15 day sacrifice period progressed. These rates of decline were substantially the same, irrespective of initial population density. Since the same number of birds were taken from each group, in approximately equal numbers per day, it appeared that the absolute increase in floor area affected the adrenal weights of both population groups in an almost equal manner.

In an effort toward clarification, a second series of regression equations were calculated in which relative adrenal weights were related to the percentage increase in floor area calculated from the first day of sacrifice (Figure 2). Removal of 20 birds from a less densely

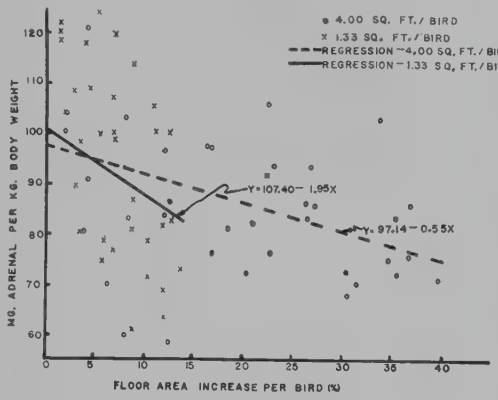
● 4.00 SQ. FT./ BIRD
× 1.33 SQ. FT./ BIRD
REGRESSION – 4.00 SQ. FT./ BIRD
REGRESSION – 1.33 SQ. FT./ BIRD
Y=107.40– 1.95X
Y= 97.14 – 0.55X
MG. ADRENAL PER KG. BODY WEIGHT
FLOOR AREA INCREASE PER BIRD (%)

FIG. 2. Effect of floor area increase on relative adrenal weight. The plotted data are individual values: 1.33 square feet per bird (X); 4.00 square feet per bird (0).

populated group resulted in a 40% increase in floor area allowed per bird while the removal of 20 birds from a densely populated group resulted in a 13% increase in floor area allowed per bird. On the basis of Figure 2 a 1% increase in floor area per bird produced a 0.55 mg per kg decrease in adrenal weights in less dense groups compared to a 1.95 mg per kg decrease in the denser groups. The difference between these two regression coefficients was significant ($P < 0.05$).

It is proposed, within the range of those data, that the adrenals of birds confined at higher population density responded more profoundly to a given increase in floor space than those less densely populated. Consideration of this in future investigations of population stress may be of aid in reducing otherwise unaccountable experimental variation.

SUMMARY

Adrenal glands of laying fowl confined for 5½ months in flocks where the floor area was 1.33 square feet per bird were significantly heavier than adrenals from those confined for the same period at 4.00 square feet per bird. The difference appeared to be due to cellular hyperplasia in the cortical areas.

Thyroid and pituitary weights were not affected by population density.

Total adrenal cholesterol was not significantly depleted in the more densely populated groups.

Adrenal weights declined progressively during the 15 days required to autopsy the 80 bird sample, regardless of initial population density. A possible explanation for this is discussed.

REFERENCES

Bressler, G. O. and R. N. Jones. 1957. Design and arrangement of equipment in the Penn State solar house. Pa. Agr. Exp. Sta. Progress Report **183**: 1-8.

Christian, J. J. and D. E. Davis. 1956. The relationship between adrenal weight and population status of urban Norway rats. J. Mamm. **37**: 475-486.

Garren, H. W. and C. W. Barber. 1955. Endocrine and lymphatic gland changes occurring in young chickens with fowl typhoid. Poultry Sci. **34**: 1250-1258.

Garren, H. W. and C. S. Schaffner. 1952. The response of young New Hampshire Red chickens to conditions to stress. Poultry Sci. **31**: 917 (abstract).

———. 1954. Factors concerned in the response of young New Hampshires to muscular fatigue. Poultry Sci. **33**: 1095-1104.

———. 1956. How the period of exposure to different stress stimuli affects the endocrine and lymphatic gland weights of young chickens. Poultry Sci. **35**: 266-272.

Juhn, M. and J. B. Mitchell. 1929. On endocrine weights in Brown Leghorns. Am. J. Physiol. **88**: 177-182.

Knobil, E., M. G. Hagney, E. J. Wilder and F. N. Briggs. 1954. Simplified method for determination of total adrenal cholesterol. Proc. Soc. Expt. Biol. and Med. **87**: 48-50.

Latimer, H. R. 1924. Postnatal growth of body systems and organs of Single Comb White Leghorns. J. Agr. Res. **29**: 363-397.

Louch, C. D. 1956. Adrenocortical activity in relation to the density and dynamics of three confined populations of *Microtus pennsylvanicus*. Ecology **37**: 701-713.

Rosenfeld, G. 1955. Steroidogenesis by intact calf adrenals perfused *in vitro*. Endocrinology **56**: 649-666.

Selye, H. 1937. Studies on adaptation. Endrocrinology **21**: 169: 188.

Snedecor, G. W. 1954. Statistical Methods. 4th Edition, Iowa State College Press.

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COQUINAS (*DONAX VARIABILIS*) ON A FLORIDA BEACH

Coquinas (*Donax variabilis* Say) are small, multicolored clams that often reach extremely high densities in the intertidal zones of various southeastern beaches. Despite their small sizes, perhaps 20 mm in greatest length, coquinas are often abundant enough to be collected for chowder. In fact, Loesch (1957) has estimated that *Donax* occasionally reaches densities of over 32,000 clams per linear yard of beach; approximately 37% of these were *D. tumida* and the rest *D. variabilis*. The west coast bean clam (*D. gouldi*) was estimated by Coe (1953, 1955) to reach densities of over 20,000 animals per square meter.

Although coquinas are quite conspicuous, at least on certain beaches, and their beautiful shells have made them favorites with collectors, they apparently have not received extensive attention of ecologists. Pearse, Humm and Wharton (1942) found them to be among the most common invertebrates on certain beaches in the Beaufort area of North Carolina. They reported that *Donax* was intertidal, moved back and forth with the rising and falling tides and reached greatest density near the low tide mark. Turner and Belding (1957), who also worked on a North Carolina beach, found that the coquinas migrated across the beach with the tide.

On Mustang Island, Texas, Loesch (1957) found a similar type of migratory behavior. According to Turner and Belding (1957) migrations of this type have been described by Mori, Jacobson and Burkenroad for various species of *Donax*. In late November of 1957 I had the opportunity of studying the distribution of *Donax* on Clearwater Beach, Florida. During the period of these observations, the coquinas did not show tidal migrations, but remained in the beach sand near the high tide mark as the tide receded.

MATERIALS AND METHODS

These studies were carried out on a 175 yard segment of beach that extended north from the Clearwater Beach fishing pier to the first groin (Breakwater). Along this section of beach, parallel to the shore line, was a ridge of sand, which was apparently piled up by wave action and marked the approximate limit of the surf at high tide. The ridge and pier represented the most stable landmarks on the beach, so all studies were made at points measured north from the pier in yards and seaward from the crest of the ridge in feet. Since no mensural equipment was at hand, all distances were measured by pacing.

Quantitative samples of beach were taken by driving a one pound coffee can into the sand; the material contained in the can, the core, was then sifted in the surf through a kitchen sieve. Each core contained about 1015 cm^3 of material and sampled 121 cm^2 of beach surface. Since the coquinas were restricted to the superficial layer of the sand, the latter appeared to be the most meaningful statistic. After the fine sand had been washed from the sample, the clams were counted by hand. Many washed cores contained coquinas almost exclusively, and thus presented no particular difficulty; however, others also contained large amounts of shell fragments from various mollusks, which made it difficult to count the clams accurately when there were small specimens present.

RESULTS

Position of the coquinas on the beach. After several days of general observations, serious studies were begun on 23 November, 1957, and continued daily until the 29th. On 23 November transects were made at positions 30, 55, 90, 125 and 160 yards north of the pier. Each transect was made up of cores taken at approximately three foot intervals from the ridge seaward to the waterline. These transects were begun at 08:30, while the tide was still out (low tide 06:52). The rising tide truncated transects made later in the morning (high tide 13:34); however, this appeared to be unimportant for the reasons detailed below.

November 24 was spent confirming the data collected the 23rd. Transects were made at 5, 25, 45, 65, 85, 105, 125, 145 and 165 yards north of the pier. Initial cores were taken approximately 9 feet seaward of the ridge; subsequent cores were at 6 foot intervals until the coquinas

were located. When the zone of coquinas was found, cores were taken at 4½ foot intervals until the zone was thoroughly sampled. A second transect was taken immediately adjacent to the main transect, but was restricted to the zone in which the clams lived.

The results of 23 and 24 November were quite similar and so have been treated as a single group of data (Figure 1). It was apparent that no coquinas lived as high

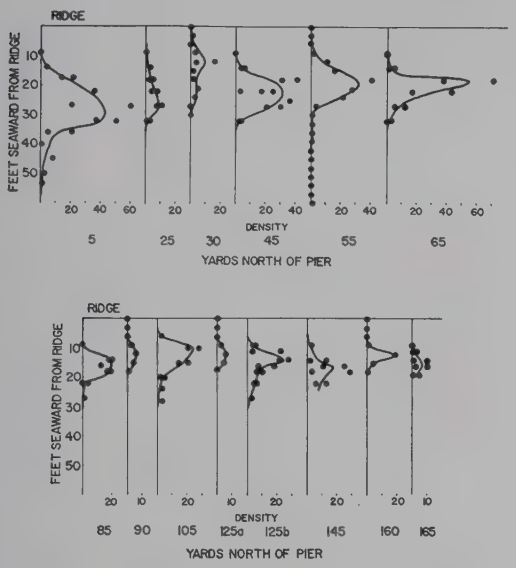

FIG. 1. Density of coquinas (*Donax variabilis*) in transects taken at various positions along Clearwater Beach, Florida on 23 and 24 November, 1957. Each transect is indicated by its position in yards north of the Clearwater Beach fishing pier. Points represent the actual numbers of clams found in a core that sampled 121 cm² of beach surface.

on the beach as the crest of the ridge. Seaward from the ridge, *Donax* began to appear in the cores at about 9 to 14 feet from the ridge. After first appearing, density in subsequent cores increased rather rapidly to a peak and then decreased toward zero. The figure shows the actual numbers of clams present in the samples and smooth curves that may explain these distributions. The curves were drawn in such a way that they appear somewhat "normal," although it seems highly improbable that an unmodified normal distribution will explain coquina densities. Several of the curves, particularly those for 5, 55, 65, 85, 105 and 125 b, were skewed with tails extending seaward. This was expected from what was observed of the natural history of these clams, which fed actively at high tide. Each wave uncovered many clams that burrowed rapidly back into the sand; a few were washed into the surf and appeared to gain positions lower on the beach as the tide ebbed.

These data suggested several other conclusions. The density of the clams appeared to be high just north of the pier, to decrease precipitously to a low at 25-30 yards north, to increase at 40-70 yards, and then to fall to a lower level through the remainder of the beach sampled (Figure 2). Figure 2 must be interpreted with care. The abscissa indicates distance of the transect from the pier, while greatest density obtained in actual sampling is

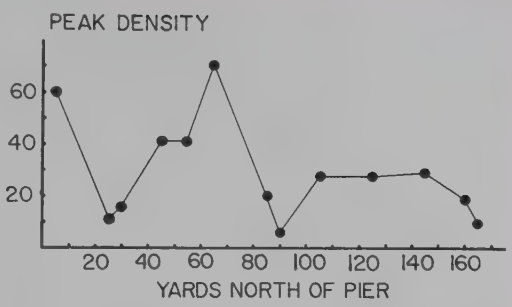

FIG. 2. Peak densities of coquinas found in transects taken at various points along Clearwater Beach on 23 and 24 November, 1957.

plotted on the ordinate. Replicate samples near a single point demonstrated that immediately adjacent areas often showed marked differences in density of coquinas; consequently, Figure 2 can only be taken as a suggestion of changes in density along the beach. The data presented in Figure 1 suggests that this high-low-high-low density pattern was also reflected by cores taken to either side of the one indicating greatest density.

Two other differences in distribution along the beach were also suggested. In the first 85 yards north of the pier the clams appeared to be farther seaward from the ridge than was true through the remainder of the beach (Table I), and the width of the zone in which they lived

TABLE I. Distance seward from ridge of first core that contained coquinas (*Donau variabilis*)

Transect	Distance from ridge (feet)
5	14
25	14
30	3
45	14
55	9
65	14
85	14
90	9
105	6
125a	9
125b	9
145	9
160	9
165	11

seemed broader near the pier than away from it.

On 25 November, at low tide, the distance from the ridge to water's edge was estimated at 20 yard intervals starting 5 yards north of the pier. These values (Table II) should give a rough indication of the slope of the beach at these points. These data suggest that the slope of the beach was quite gentle near the pier, became progressively more steep to the north, and then became shallower again as the groin was approached. Although the nature of these data preclude specific conclusions, it seems probable that conditions near the pier, which either resulted from or were reflected in the shallower slope of the beach, were somewhat more favorable for *Donax* than they were further north. It seems probable that the apparent greater width of the zone near the pier resulted from the shallow slope, which would produce a broader

TABLE II. Distances from the ridge to water's edge at 20 yard intervals north of the Clearwater Beach fishing pier at low tide on 25 November, 1957

Position (yards North of pier)	Distance (feet)
5	75
25	60
45	57
65	57
85	54
105	46
125	45
145	51
165	63

area washed by the surf. This gentle slope was, no doubt, the result of the wave-breaking action of the pier.

Depth of Coquinas in the Sand

On 25 November, when a storm from the northwest and lowered temperatures precluded general observations, a concentrated study of the depth to which coquinas burrowed was made. Samples were taken from various depths at a point about 45 yards north of the pier. The first core was taken to a depth of about 1½ inches below the surface, the second from 1½ to to 3 inches, and the third from 3 to 4½ inches. The clams were largely restricted to the superficial 1½ inches of sand (Table III). It seems probable that the 3 animals found at greater depths were driven down into the sand by the can while the core was being taken.

TABLE III. Numbers of coquinas at various depths of sand on Clearwater Beach. These cores were taken near an area of high density about 45 yards north of the fishing pier on 25 November, 1957

	Distance Seaward from Ridge (feet)						
	12	15	15	15	18	18	18
Depth in sand (inches)	Numbers of Coquinas per Core						
0-1½	3	50	55	54	47	42	42
1½-3	0	0	0	0	1	0	0
3-4½	0	0	0	1	0	0	1

Effects of a Storm and Its Aftermath

The storm, which continued through the night of 25-26 November, washed almost all of the coquinas from their zone on the beach. By the morning of 26 November the storm had subsided considerably, although the surf was heavy. Through 26 and 27 November repeated transects were made at a point about 50 yards north of the pier. Because the coquinas were essentially absent from the sand, the transects were extended well into the surf (Table IV). The samples of 26 November indicated that the coquinas moved up and down the beach with the rising and ebbing tide. They remained in the surf, and did not re-establish themselves in the sand until the morning of the 27th when they were found in the lower portion of the intertidal zone. Some were still in the surf. That afternoon they were higher on the beach in the surf of the rising tide. The clams had become well established in the sand by the 28th, so transects were run at 50, 100 and 150 yards (Table V).

TABLE IV. Numbers of coquinas at various periods after wash-out caused by storm of 25-26 November, 1957. All transects were made at a point approximately 50 yards north of the Clearwater Beach fishing pier. Each figure represents number of coquinas per core

	Number per Core						
	26/xi/57				27/xi/57		28/xi/57
Date and time	12:00	14:00	15:25†	17:30	09:30	16:00	10:00
Distance from Ridge (in feet)							
9	0	0	0	0	0		
15	0	0	0	0	0		0
21	1	0	0	0	0		0
27	0	0	0	0	0	0	0
30	—	—	—	0	—	—	0
33	0	0	0*	0	0	0*	0
36	—	—	1	0	—	0	4
39	0	1*	47	0	0	0	0
42	—	6		0	—	5	19
45	0	47		2*	1	8	54
48	—	70		25	2	34	189
51	0	26		41	49		24
54	—			33	43		0
57	3*				39		2
60	27				6		2
63	55				11‡		—
66	107				29‡		0
69	94				18*‡		—
72					1		0*
75					1		—
78					7		0
81					7		—
84					0		0

* Surf line.
† High tide.
‡ Clams mostly small.

On 29 November, although it was impossible to run transects at ebb tide, 3 truncated transects were obtained during the rising tide. In each case cores that contained clams were obtained from points well above the surf, indicating that the coquinas were established in the sand. The data for these 2 days suggested that the coquinas were moving up the beach toward their former position (Figure 3). In the wake of the storm the high tide line was considerably below its previous mark, which probably slowed the establishment of the clams at their former position.

Discussion

Although generalizations from short-term studies are often dangerous, and the data presented do not lend themselves to precise analysis, certain conclusions seem warranted. The coquinas appear to occupy a relatively stable zone on the beach, which appears to be close to the high tide mark. The rising tide activates the clams when it reaches this zone, and the surf, washing over the clams, provides food and aeration. Each wave washes many animals from the sand. As the surf subsides, the uncovered clams burrow immediately into the soft sand. The ebbing tide leaves the clams high on the beach, and inactive in the sand until they are activated by the next high tide. At low tide the zone is marked by the presence of small holes in the sand where the coquinas have burrowed.

TABLE V. Numbers of coquinas in cores of transects of Clearwater Beach made on 28 and 29 November, 1957

	NUMBERS OF COQUINAS					
	28/xi/57			29/xi/57		
Yards North of pier	50	100	150	50	100	150
Feet from ridge						
15	0	—	—	—	—	—
18	—	—	—	—	—	0
21	0	—	—	—	—	—
24	—	—	—	—	—	0
27	0	—	—	—	—	—
30	0	0	0	0	0	0
33	0	—	—	—	—	—
36	4	0	0	3	3	0
39	0	—	—	33	35	5
42	19	2	0	110*	23*	9
45	54	—	—	—	—	*
48	189	22	5			
51	24	28	12			
54	0	15	5			
57	2	4	0			
60	2	—	—			
63	·	1*	0			
66	0	—	—			
69	—	0	0			
72	0*	—	0*			
75	—	0	0			
78	0	—	—			
81	—	—	0			
84	0	—	—			

* Surf line.

The heavy surf of storms disrupts this pattern of activity. As the beach is pounded by the waves, the clams are washed away faster than they can burrow back into the sand and are unable to maintain their position near the high tide mark. Under these conditions they appear to move across the beach with the tides, eventually gaining a foothold and establishing a zone along the beach. Once washed from their zone it may take them several days to become re-established in their pre-storm position. This rate of re-establishment is certainly affected by strength of surf and may be controlled by abnormally low or high tides.

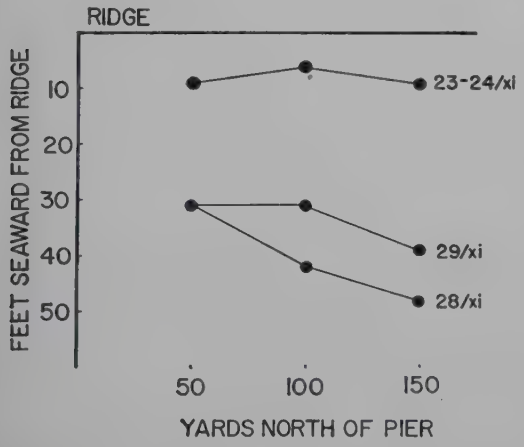

FIG. 3. Position of zone of coquinas on Clearwater Beach on 23-24, 28, and 29 November, 1957. The position of the zone is indicated by the highest point on the beach at which coquinas were found.

Certain of these data, and their interpretations, differ markedly from those of previous workers (Loesch 1957, Turner & Belding 1957). Under normal conditions on Clearwater Beach the coquinas appeared to live in a rather distinct zone and were not found to ". . . move back and forth more or less with rising and falling tides," (Pearse, Humm and Wharton, p. 174) as they did at Beaufort, Wrightsville Beach, N. C. (Turner & Belding) and on Mustang Island. The discrepancy between the data reported here and those of other workers is difficult to explain, particularly in the light of the behavioral mechanisms described by Turner and Belding, which would favor tidal migration. These differences may have been related either to slope of the beach, the amount of surf, both factors, or perhaps, localized differences in behavior.

Pearse, Humm and Wharton also indicated that the clam population was most dense near the low tide mark at Fort Macon, whereas at Clearwater greatest density was near the high tide line. This difference could have resulted from a heavier surf at Fort Macon. If most of their observations had been made at low tide, one would expect few coquinas to gain foothold on the upper beach in a relatively heavy surf. Thus, had their studies been made at ebb tide, density would be expected to be low in the intertidal zone and only increase at the approximate water line. On Bird and Sheepshead Shoals, which were inundated at high tide, Pearse, Humm and Wharton found the greatest density near the high tide mark. Although Loesch was not directly concerned with the vertical distribution of coquinas, he does note that occasional individuals were trapped in the sand above low tide; he indicates that clams may be as much as 14 yards above the low tide mark.

Pearse and his colleagues expressed the density of *Donax* on the basis of numbers per unit volume of sand. Their most convincing data came from beach siftings. Their sieves, which had a 6½ liter capacity, were filled with a spade. Since the present data indicate that coquinas live in the superficial layers of the sand, a spade would unselectively gather material that would not be expected to contain coquinas under any circumstances. Thus such density data would appear to have little meaning beyond suggesting differences in relative density. Coe's expression of density in terms of surface area is more meaningful, as, perhaps, is Loesch's designation in terms of linear measure of beach. I have, however, resisted the impulse to extrapolate these data to estimates of numbers of animals per unit of surface area, because replicate samples from regions of peak density indicated considerable lack of homogeneity within quite restricted areas.

SUMMARY

On Clearwater Beach, Florida, during the last 2 weeks in November, 1957, coquinas (*Donax variabilis* Say) were found to inhabit a zone that appeared just seaward of the high tide mark. Transects cross the zone suggested a skewed distribution that roughly approximated a normal curve with the tail extending toward the water. The segment of beach studied extended north about 175 yards from the Fishing Pier. The density of clams seemed highest near the pier. As one progressed northward from the pier density dropped to a lower level. Near the pier, the zone of coquinas seemed to extend farther seaward and appeared to be broader than was the case farther

to the north. During the study the clams were washed out of this zone by a storm; after some 36 hours of moving back and forth across the beach in the surf, they became re-established in the sand and appeared to be moving back toward their former position when they were washed out by a second storm. The coquinas inhabited only the superficial 1½ inches of sand.

Acknowledgment

I am indebted to D. W. Calhoun and Dr. Orlando Park who have made a number of suggestions on the treatment of these data, and to my wife for assistance in the field. An anonymous editorial referee was kind enough to call my attention to two references that would otherwise have been missed.

References

Coe, W. R. 1953. Resurgent populations of litteral marine invertebrates and their dependence on ocean currents and tidal currents. Ecology **34**: 225-229.

———. 1955. Ecology of the bean clam (*Donax gouldi* on the coast of Southern California. Ecology **36**: 512-514.

Loesch, H. C. 1957. Studies of the ecology of two species of *Donax* on Mustang Island, Texas. Publ. Inst. Marine Sci. **4**: 201-227.

Pearse, A. S., H. J. Humm and G. W. Wharton. 1942. Ecology of sand beaches at Beaufort, North Carolina. Ecological Monographs **12**: 135-190.

Turner, H. J., Jr. and D. L. Belding. 1957. The tidal migrations of *Donax variabilis* Say. Limnology and Oceanography **2**: 120-124.

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MODIFICATION OF THE HAYWARD ORANGE-PEEL BUCKET FOR BOTTOM SAMPLING[1]

Introduction

The Hayward orange-peel bucket has been utilized since 1914 (Sumner *et al.* 1914) as a sampling device for quantitative marine benthic studies, but its use has not been widespread until quite recently. This piece of equipment is manufactured for use in construction work,[2] but it is necessary to alter it for use as a bottom sampler. The modifications utilized in the past have varied, but none of them has been adequately described.

The advantages of this sampler are many, (1) ease in operation, (2) commercially manufactured in a variety of sizes, (3) made from drop forged steel, (4) no messenger required to activate the tripping mechanism, (5) of sufficient weight for good penetration, and (6) a sample of the undisturbed top layer may be obtained by reaching through the skirt opening before the bucket is emptied.

The disadvantages of the Hayward orange-peel bucket were recently outlined by Thorson (1957); these included, (1) a second cable required or slack mechanism activated by a messenger necessary for closure, (2) active washing of the surface area when hauling to the surface, (3) jaws seldom close tightly and rocks or bivalves prevent closure, (4) in soft bottoms the substrate gets into the closing mechanism, and (5) it is difficult to ascertain the exact surface area covered. Of the disadvantages listed, items one and two have been overcome by the present design. Barnard, *et al.* (1958) have worked out a relationship between the volume and surface area sampled thus correcting item 5. Points 3 and 4 are justified but the closure of the jaws could be made more secure by the addition of overlaps on each of the blades; however, this has not been done as yet. Rocks and other hard objects encountered affect the closure of all bottom sampling devices. Recently Dr. D. E. Hurley of the New Zealand Oceanographic Institute wrote me of the addition of plates at the top of the blades shielding the closing mechanism from the substrate.

The modifications described herein are the results of the gradual accumulation of ideas by many individuals. Chief among these was Mr. Charles Horvath who devised the trigger mechanism which eliminated the second cable and/or messenger. Photographs of the bucket have appeared in Anon (1955), Hartman (1955), Reish (1955), and Sumner, *et al.* (1914).

Modifications of the Orange-Peel Bucket

The measurements described below apply to the size one bucket; however, these modifications would apply to the larger samplers by making the necessary adjustments.

Trigger Mechanism

The specifications for the brass cylinder are indicated in Figures 1 and 2. The eye-bolt and trigger knob are in direct line with one another and are threaded for attachment to the cylinder. The cable from the winch fastens to the eye-bolt. The trigger knob fits into the eye of the handle which is part of the original bucket. A brass plate, measuring ½ X 2 X 4 inches, is welded to the back side of the handle. A small hole is drilled through this plate for attachment of a 2½ inch coiled spring from the sleeve (see below).

Cable

The cable should be replaced by a three-sixteenths inch flexible stainless steel one, of approximately 3 feet in length. The cable is welded to the toggle (Figure 1) which is fastened to the bolt in the trigger mechanism. The opposite end of the cable is fastened to the pulley as originally, with the addition of filling the space within the pulley with lead to prevent the cable from slipping out.

Skirt

The purpose of the skirt is to minimize the amount of washing of the sample as it is being raised to the surface. Denim, canvas, or sail cloth have been used

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[2] Available from the Hayward Co., 50 Church St., New York, New York.

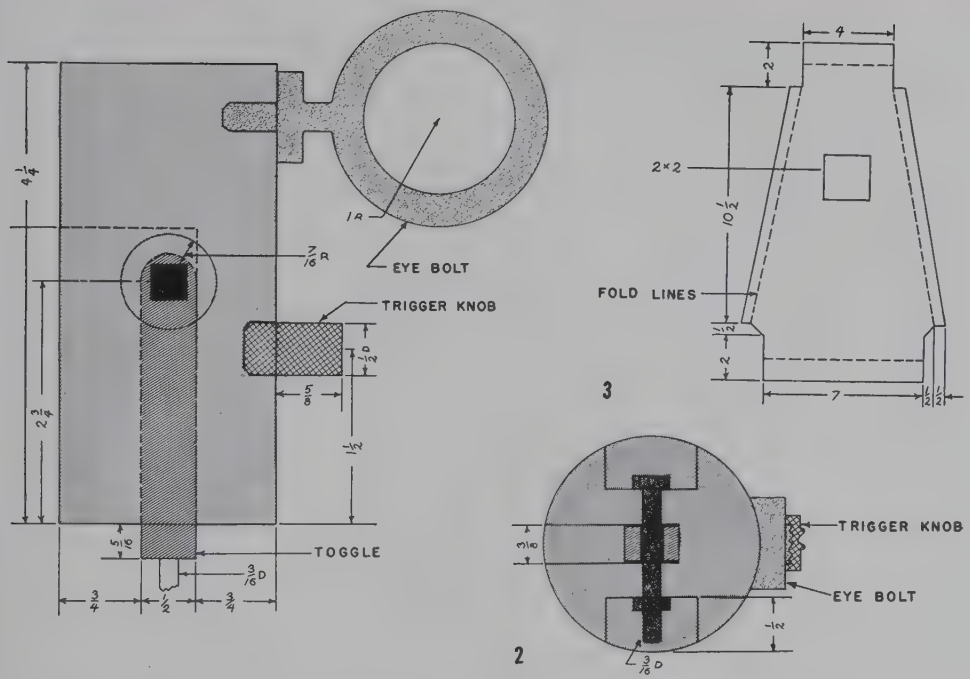

FIG. 1. Side view of the trigger mechanism for the size one Hayward orange-peel bucket.
FIG. 2. Top view of the trigger mechanism; trigger knob and eye bolt only partially shown.
FIG. 3. Pattern for one panel of skirt for the size one Hayward orange-peel bucket.

as material for the skirt. The skirt pattern is given in Figure 3. Four pieces are needed to complete the skirt. In addition, 4 flaps measuring 4 X 5 inches are required to cover each opening in the skirt paneling. The 4 panels are sewed together. The upper flap of the skirt is sewed around a stainless steel sleeve measuring ½ inch wide, 1/32 inch thick, and 4½ inches in diameter. Brackets made from the same stainless steel sheeting and measuring ¾ X 1½ inches are riveted to the sleeve opposite one another. A hole is drilled in the shorter end to fit to the bolt of the bucket securing the upper portion of the skirt to the sampler. One-fourth inch holes are drilled at opposite ends of the upper portion of each blade. The bottom flaps of the skirt are hemmed and sailmakers islets are fastened to correspond to the holes in the blades. The skirt is fastened to the blades by winged nuts and bolts.

Operation

The first operation of the bucket is to set the trigger as described above. The bucket is lowered into the water and upon contact with the bottom, the sampler is raised which closes the blades immedately.

Care

The bucket should be washed in fresh water after using and all moving joints and the two chains greased. Periodically the bucket should be dismantled and reassembled to assure that all the parts are in good working order.

SUMMARY

The modifications of the commercially manufactured Hayward orange-peel bucket for biological bottom sampling are described and figured. The advantages and disadvantages of the apparatus are discussed.

REFERENCES

Anon. 1955. Instruction manual for oceanographic observations. U. S. Hydrographic Office Publ. No. 607, Second Edition.

Barnard, J. L., Olga Hartman, and G. F. Jones. 1958. Benthic ecology of the mainland shelf of southern California: Biomass and communities. State of California, Water Pollution Control Board Publication. [Mimeographed report].

Hartman, Olga. 1955. Quantitative survey of the benthos of San Pedro Basin, southern California. Part 1. Preliminary results. Allan Hancock Pacific Exped. **19**: 1-185.

Reish, D. J. 1955. The relation of polychaetous annelids to harbor pollution. Public Health Repts. **70**: 1168-1174.

Sumner, F. B., G. D. Louderback, W. L. Schmitt, and Edward C. Johnson. 1914. A report upon the physical conditions in San Francisco Bay, based upon the operations of the United States fisheries steamer "Albatross" during the years 1912 and 1913. Univ. of Calif. Publ. Zool. **14**: 1-198.

Thorson, Gunnar. 1957. Sampling the benthos. **In** Treatise on Marine Ecology and Paleoecology, vol. I, Edited by Joel W. Hedgpeth, pp. 61-86.

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DENSITY AND DISPERSAL IN LABORATORY CRAYFISH POPULATIONS

That dispersal is related to population density with movement away from high density centers, is a widely held ecological concept which has been challenged recently, notably by Andrewartha and Birch (1954). They cite investigations supporting the view that dispersal is an innate tendency not necessarily related to density. While additional, corroborative studies may be found, other data may be interpreted as evidence for the population pressure concept. The general problem of dispersal has been reviewed by Heape (1931), Wolfenbarger (1946), and Elton (1958) among others, but in truth the large numbers of investigations take almost no cognizance of the density factor and the few interpretations made are conflicting. A critical review of dispersal relative to density is needed, but the purpose of this paper is to report on an experimental approach to the problem.

Experimental Procedure

The animal used was *Cambarus alleni* Faxon, a Florida crayfish amenable to laboratory culturing (Bovbjerg 1956a). The animals were well fed, healthy adults of both sexes; newly molted individuals were not used. Experimental animals were collected randomly from the culture tank; therefore some animals were used in more than one experiment. In the case of single animal controls, each was marked and not re-used.

The experimental environment was a water table measuring 3 meters by ¾ of a meter which was converted into a 13 meter trough or chute with a continuous aluminum partition as indicated in Figure 1. The

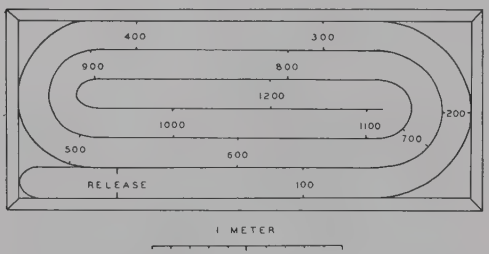

Fig. 1. The linear experimental environment on water table; distance from release point in cm.

width of the trough was approximately 20 cm, and it was marked at 10 cm intervals from 0 to 1300. The substratum was fine white sand; the water of 10 cm depth was aerated vigorously prior to each experiment, ensuring a saturated oxygen content. Light was from 4 overhead fluorescent units and was approximately uniform with some slight shadowing along the walls of the trough. Room temperatures were identical in the culture and experimental tanks. These conditions describe an extremely monotonous environment; it was linear in nature but sufficiently wide for individual crayfish to pass each other while not allowing of significant lateral movement. All data recorded are distance from release. It was hoped that this reduction of environmental variables would emphasize the effects of crowding as a specific biotic interaction.

The experimental procedure was not complex. Twenty-five groups of 5, 10, and 20 animals were released at one end of the chute by opening a gate at the zero mark; a few minutes of acclimatization preceded each experiment. At successive 5 minute intervals, the position of each animal was recorded on a map. Most of the experiments were of one hour's duration but some of each population size were allowed to continue for a longer time. Twenty-five single animals were run as controls.

A duplicate set of 100 experiments was done with one environmental change. At every half meter a small flower pot (large enough for one crayfish) was placed on its side facing out from the wall of the chute. This altered the situation in furnishing refuge not only within but along the sides of each pot.

From these approximately 10,000 position recordings were computed the mean distances from release for each experimental population at successive 5 minute intervals. From the 25 experiments at each population size, a mean of means for each 5 minute interval was calculated. These data, for populations varying in initial density, should indicate whether density as such plays a role in the rate of dispersal for this species.

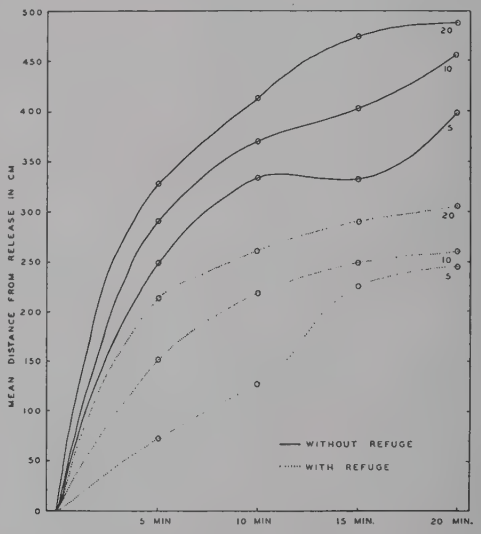

Fig. 2. Mean distance moved by populations of 5, 10, and 20 animals recorded at 5, 10, 15, and 20 minutes; data presented for experiments with and without refuge.

Results

The results (Figure 2) support the generalization that the dispersal of the experimental animals was directly related to the initial density; this was true for the groups with and without refuge. The curves of the graph represent mean distances from release point of each of the experimental populations at successive time intervals, therefore rates of dispersal. Individual variability was the rule; some remained at the release point while certain active animals progressed steadily far up the chute. This was very apparent in the single animal controls where variability of behavior was most manifest although the distance moved tended to be less than the mean for the 5 animal populations.

As the individuals dispersed and local density decreased, there was little difference in rates of movement in the various sized populations. After the first 20

mintues the density at any one point was low even for the largest group. Longer periods of observation revealed little increase of the mean distance; this fluctuated as individuals began to move freely in both directions. After one hour, mean distance approached equality for all 3 populations.

Subjectively, differences in behavior were evident; with increasing population size two phenomena became more prominent. First, the direct movement away from the release point was far more obvious in the larger populations. At the 20 animal density, the first few minutes gave an impression of population streaming. Secondly, the number of tension contacts (avoiding, threatening, striking, and fighting) was highest at the higher initial densities. Such tension contacts rarely occurred in the 5 animal populations.

The difference in rates of dispersal between the groups with and without refuge are striking. The movement of the smallest group without refuge was greater than the largest group with refuge. Without refuge, the 20 animal group reached 400 cm in 10 minutes; the 10 animal group reached this point in 15 minutes; while the 5 animal group came to this point only after 20 minutes. In contrast, the groups with refuge reached only 250 rather than 400 cm in approximately the same times.

Clearly the first 5 minutes following release is the time of greatest outward dispersal for both sets of experiments (Figure 3). Here one sees best the obvious differ-

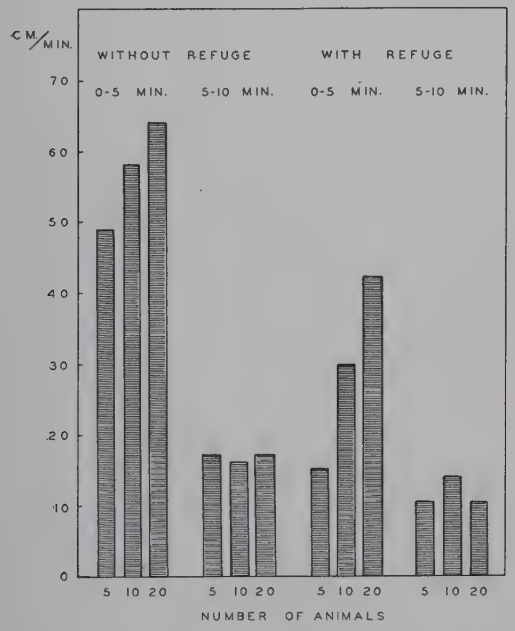

FIG. 3. Comparative rates of movement in cm per minute for first and second 5 minute intervals; data presented for experiments with and without refuge.

ence between the groups with and without refuge. One further observation is important. The disparity in rates of dispersal is greatest in the groups with refuge. In both sets of experiments the differences between the 5 and 20 animal groups are significant, for those without refuge, a probability of less than .05, and those with refuge, less than .01.

CONCLUSIONS

The movement away from a density center should be described as a kinesis, random activity induced by a particular stimulus. The net shift tends to be away from sub-optimal conditions. This activity appears to fit what Allee *et al.* (1949) describe as "population pressure resulting from coactions." The stimulus to disperse is social. Crayfish exhibit awareness of others; they display aggressive behavior in the field and in laboratory tanks. The cues to this behavior are both visual and tactile (Bovbjerg 1953, 1956 b; Lowe 1956). So enough is known of the ecology and behavior of crayfish to propose that crowding is the sub-optimal situation from which there is a population shift.

The disparity in activity in groups with and without refuge is considerable. The general slower movement with refuge present is clearly a function of the occupancy of these refuges and subsequent immobility of the occupants. But the intriguing problem is the increased effect of density when refuge is available. In the non-refuge groups the individuals would seem to be stimulated by two factors; first, the need for space free of other crayfish and secondly, though related, the need for refuge. The introduction of flower pots furnishes refuge and reduces the variables more specifically to space needs.

Is this an instance of competition? The commodity initially in short supply is space. In this sense, there is competition directly for that space and the result is an altered population density as a function of dispersal. The same conclusion was reached by Crombie (1944) in his study of grain beetles where emigration occurred as a direct response to crowding and subsequent fighting.

To extrapolate may be dangerous but it is probable that other crayfish would demonstrate dispersal patterns similar to those of *C. alleni*. Such a pattern may be characteristic of many decapod crustaceans, since similar aggressive behavior is known for many marine littoral crabs and for the lobsters.

A general hypothesis is proposed. Animals demonstrating intra-specific aggressive behavior, territoriality, or spacing will disperse in such a density related fashion. Conversely, those species without these behavioral attributes will disperse in a manner not related to density or fail to disperse as might be the case in forms tending to aggregate. Such an eclectic position must necessarily be re-examined after further experimentation with many and widely divergent forms.

SUMMARY

1. Experiments were designed, using laboratory crayfish populations, to determine the role of density relative to dispersal rate in a linear environment.

2. Populations of 5, 10, and 20 animals revealed a direct relationship between initial density and rate of movement, particularly in the first 5 minutes.

3. The basis of this population pressure effect is an intraspecific coaction stemming from the aggressive behavior characteristic of crayfish.

4. It is proposed that similar dispersal patterns would be found in other species displaying aggressive behavior of this sort; conversely, such dispersal traits would be lacking in groups without such aggressive behavior.

REFERENCES

Allee, W. C., A. E. Emerson, O. Park, T. Park, K. P. Schmidt. 1949. Principles of Animal Ecology. Philadelphia.

Andrewartha, H. G. and L. C. Birch. 1954. The Distribution and Abundanceof Animals. Chicago.

Bovbjerg, R. V. 1953. Dominance order in the crayfish *Orconectes virilis* (Hagen). Physiol. Zool. **26**: 173-178.

———. 1956(a). A laboratory culture method for crayfish. Ecology **37**: 613-614.

———. (1956(b). Some factors affecting aggressive behavior in crayfish. Physiol. Zool. **29**: 127-136.

Crombie, A. A. 1944. On intraspecific and interspecific competition in larvae of gramnivorous insects. J. Expt. Biol. **20**: 135-151.

Elton, C. 1958. The Ecology of Invasions. London.

Heape, W. 1931. Emigration, Migration and Nomadism. Cambridge.

Lowe, M. E. 1956. Dominance subordinance relationships in the crawfish *Cambarellus shufeldtii*. Tulane Stud. Zool. **4**: 139-170.

Wolfenbarger, A. 1946. The dispersion of small organisms. Am. Mid. Nat. **35**: 1-152.

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AQUATIC BIOTAS OF TEASEL WATERS

The teasel (*Dipsacus sylvestris*) has opposite leaves with the bases of each pair joining to form a cuplike structure capable of holding water. The biotas of a number of such "teasel waters" in the region of Ithaca, N.Y. were examined during the summer of 1956. All teasel plants from which axil water was surveyed were growing on high ground so that the water in their axils must have been rain water, and their biotas must have crossed dry land to reach them.

The frequences of occurrence of various organisms in 186 axils (113 plants) are given below:

% occurence	*Organism*
97	Illoricate rotifers
73	Hypotrichs
67	*Colpoda*
49	*Cyclidium*
43	Nematodes
28	Rhabdocoels
22	Holotrichs (unidentified)
18	*Breslaua*
15	*Spathidium*
9	Filamentous algae
8	Tardigrades
5	*Aeolosoma*

Small, green, spherical, unicellular algae were also common.

There was considerable irregularity in the occurence of most of these organisms. When comparing areas however, it could be seen that the frequency of occurrence of some organisms was quite different for different areas. For example, in one area 34 plants were sampled and 9 (26.4%) were found to contain tardigrades, but tardigrades were not found in any of the 79 plants which were sampled in other areas. On the other hand, only 50% of the plants of this area contained hypotrichs, while 83.6% of the plants of other areas had them.

Teasel waters have such disharmonic biotas because the time available for their colonization is very limited (they usually do not persist much longer than 2 months). This is in contrast to the situation on oceanic islands where biotas are disharmonic because of the great distances isolating them.

The short time required for colonization of teasel axils and similar isolated bodies of water means that, unlike oceanic islands, the processes and courses of colonization are easily amenable to effective observation and experiment. In addition to delincation of the mechanisms of overland dispersal by small aquatic organisms, such studies may shed light on many hypotheses concerning mechanisms of dispersal of terrestrial organisms to oceanic islands.

The surface area of the water in teasel axils seldom exceeds about 25 cm^2 and is commonly less than 1 cm^2. The high frequency with which some organisms reach these tiny waters within a month or so shows that their mechanisms of passive dispersal must be very effective. This is especially true because the method of estimating an organism's vagility by recording its presence in specific isolated environments is likely to give results which are low. A species living successfully in an isolated environment such as the water in the axil of a teasel, must not only have been transported overland to the teasel axil, but also must have entered the teasel axil community. It may have had to effect this entrance into the community against pressures such as competition and predation. In addition it must have been able to survive and reproduce in spite of possible environmental extremes (high temperature and low oxygen are common in teasel axil waters).

An extended program is underway in central Texas to investigate further, under controlled conditions, the various aspects of overland dispersal of small aquatic organisms. This includes study of factors influencing colonization of isolated environments as well as the study of the dispersal mechanisms themselves.

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RECORDS OF THE SEA-SIDE ISOPOD *LIGIA OCEANICA* AT CAPE ANN, MASSACHUSETTS

Records of the sea-side isopod, *Ligia oceanica* (L.), on the New England coast have been reviewed by Swan (1956). In addition to reviewing the literature, he added some records of his own from the coast of Maine. Specimens collected at Woods Hole, Massachusetts, by W. C. Allee and his students (Allee 1919, 1923), not included in the Swan report, should be added to the compilation.

The only published records for Cape Ann, Massachusetts, are those mentioned by Swan (*i.e.* a cast skin from the rocks of East Gloucester collected by Dr. C. H. Blake and a collection made by Dr. Richard Dow from Rockport, listed without data). The writer has been engaged in studies on the marine life at Cape Ann since 1933. On August 15, 1947, I collected for the first time a few specimens of *Ligia oceanica* from a stone foundation beneath the Gorton-Pew wharf in East Gloucester. These were collected in crevices of the sea-wall during low tide. In 1956 I discovered a very large population of this species inhabiting the crevices of the stone blocks which compose Dog Bar Breakwater in Gloucester Harbor. This population was sampled during the following 2 summers during which time the population maintained its large number. Specimens of all sizes from the newly hatched to a body size of 32 mm exclusive of the uropods were found. Females carrying juveniles and very large male specimens were common. They were found primarily under wet boards, paper, cardboard, and seaweeds which had been washed into the crevices of the granite blocks. More specimens were collected on the harbor side of the breakwater than on the ocean side. The harbor side, facing the north, was shaded and more humid; there was also more organic debris on the harbor side. At low tide specimens were found in crevices extending downward for 3 tiers of stone blocks but were seldom found on the fourth tier even though it was out of water at the lowest tide period. Each block has a height of about 3 feet. The greatest density of population was centered between the second and third tiers from the top.

While quantitative samples were not made because of the secretive habits and very rapid motion of Ligia when exposed, it appeared that the population in 1958 was somewhat larger than in 1956 and 1957. Several winter storms during the preceding season may have reduced the rat population on the breakwater. These rats are probably the only major enemy of Ligia. In addition to fungal growth and decomposing organic matter under which they hide, Ligia appears to feed on dead fish, crabs, and bait abandoned by fishermen (worms, crushed snails, mussels, and clams).

In 1958 a search was made for Ligia in other sections of Cape Ann. None was found in the sea-wall bordering the northern boundary of Gloucester Harbor, and none was found among the boulders, stone piers, and stone walls along the Annisquam River (tidal inlet) or at Annisquam Harbor and its adjoining coves. In August of 1958 the writer with John Auditore examined stone piers along the shoreline of inner Gloucester Harbor. Here specimens were found commonly in shaded, moist crevices where abundant organic debris had accumulated. By removing planks from the wharf at the Cape Ann Seafoods Company, we found an abundant population. It is very probable that all of the fish wharves contain an abundance of this very large terrestrial isopod which is found only along the margin of salt water.

The identification of the species was confirmed by Dr. Thomas E. Bowman, and the manuscript was critically read by Dr. Bowman and Dr. Fenner A. Chace, Jr., both with the Division of Marine Invertebrates at the U. S. National Museum.

References

Allee, W. C. 1919. Studies in Marine Ecology, I, The Distribution of Common Littoral Invertebrates of the Woods Hole Region. Biol. Bull. **44**: 180.

———. 1923. Studies in Marine Ecology, IV, The Effect of Temperature in Limiting the Geographical Range of Invertebrates of the Woods Hole Littoral. Ecology **4**: 344.

Swan, E. F. 1956. Isopods of the Genus Ligia on the New England Coast. Ecology **37**: 204-206.

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THE DISTRIBUTION OF THE ESTUARINE ISOPOD, *CYATHURA* SP., ALONG THE EASTERN COAST OF THE UNITED STATES[1]

Well over a hundred years ago, Gould (1841) and De Kay (1843) listed in faunal reports from Massachusetts and New York respectively an isopod, *Anthura gracilis*. Apparently, in 1855, Stimpson named the same form *Anthura polita* and Harger (Verrill and Smith 1874) called it *Anthura brunnea*.

Although Harger (1878) realized that his *A. brunnea* was probably synonymous with *A. polita*, he also noted that the species of isopod he had discovered seemed to fit the description of *Cyathura carinata* (Krøyer), specimens of which he had never seen. In spite of the striking morphological similarity of *C. carinata* (K.), described from northern Europe, to *A. polita*, Harger (1879) made the following statement about the American anthurid saying that it was "A southern species, not found north of Cape Cod until the summer of 1878, when it was taken at Gloucester, Massachusetts. Usually found among eel-grass or mud in shallow water."

Until its discovery at Gloucester, *A. polita* had previously been found only in southern and central United States at Norfolk, Va. (Stimpson 1855), Great Egg Harbor, N. J. (Verrill and Smith 1874), New York state (Gould 1941), and Vineyard Sound (Verrill & Smith, 1874). However, in 1886, Norman and Stebbing, and later, Richardson in 1905, indicated that *A. gracilis* DeKay, *A. polita* Stimpson, and *A. brunnea* Harger were actually synonymous with *Cyathura carinata* (Krøyer).

[1] This work was supported by the McCandless Fund of Emory University and an Office of Naval Research-Marine Biological Laboratory Institutional Grant.

According to the contemporary literature dealing with this species, the distribution of *C. carinata* (K.) includes the eastern coasts of North America, Greenland, western Europe (Richardson 1905, Stephenson 1948), the Mediterranean (Stammers 1932), West Africa (Monod 1925), South Africa (Barnard 1925, Day *et al.* 1952), China (Tattersall 1922), and Asiatic Russia (Gurjanova 1936).

One conclusion suggested by this recorded distribution of *C. carinata* (K.) is that the east coast North American *Cyathura* is a northern form (Allee 1923) rather than a southern one as Harger had contended. However, a recent examination of our east coast North American species[2] and a comparison of it with *C. carinata* (K.) from the type location[3] show that our species found from Lake Ponchartrain, La. to Chewonki Creek, Maine (Figure 1) is, indeed, not Krøyer's species, but a new undescribed one. Also, Dr. Torben Wolff of Denmark (private communication) finds no authentic record of *C. carinata* (Krøyer) from Greenland. Apparently, then,

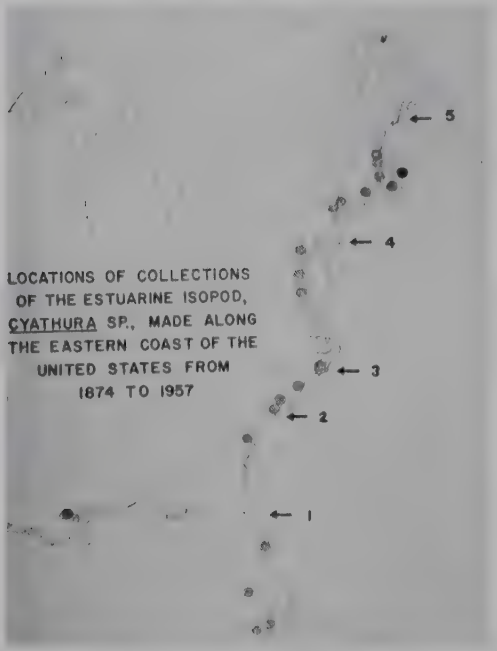

FIG. 1. Locations of collections of the estuarine isopod, *Cyathura* sp., made along the eastern coast of the United States from 1874 to 1957. Grey dots represent locations of specimens in the U. S. National Museum, unshaded ones collections by the author, and the black dot represents approximately 40 collections on Cape Cod, Mass. and vicinity.

[2] Dr. Milton A. Miller of the University of California (Davis) has examined the specimens from the U. S. National Museum, those collected by the author, Denmark, Germany, and South Africa (courtesy of K. H. Barnard). He and the author are preparing a monograph on the new species including the systematics, distribution, and ecology of the genus, *Cyathura*.

[3] Specimens sent to us by Drs. T. Wolff and E. Rasmussen of Denmark and Dr. A. Panning of Germany.

either some other anthurid taken in Greenland must have been mistaken for *Cyathura* or there is an error in the literature.

Since *C. carinata* (K.) and the east coast North American *Cyathura* are only two of several species of the genus, *Cyathura* (Barnard 1925, Monod 1925), it has occurred to us that our species and the European-Asian form may have arisen from a common preglacial species which possibly had a circumpolar distribution. When the original species was subdivided once or many times by lobes of glaciers during the last ice age and driven south, speciation may have occurred. Now, during the present interglacial period, populations of *C. carinata* (K.) and the North American *Cyathura* sp. may be moving north again. This is further borne out by the absence of cyathuras from Norway and the appearance of *C. carinata* (K.) (Löwegren 1937, Lundström 1937) in Sweden in the 1930's—remembering that the American form got only as far as Gloucester, Mass. in 1878. Also, no cyathuras have been taken in the Gulf of St. Lawrence or Baie des Chaleurs (Bousfield 1955, and E. L. Bousfield and P. Brunel, private communication). During the month of August, 1958, the author made an unsuccessful attempt to collect the North American *Cyathura* sp. along 900-1000 miles of the south bank of the St. Lawrence River and both sides of Cape Breton Island and thus verify Ganong's suggestion made in 1890 that relict invertebrates of a so-called "Virginian" fauna might be found in the Gulf of St. Lawrence. Some 30 stations were chosen for study because they appeared to be very similar, from the standpoint of tidal range, salinity, and vegetation, to the tidal marshes along the east coast of the United States where cyathuras were found; however, the substrates composed of shalely gravel, decomposed red standstone, and silty clay were quite different from those found in central Maine southward. Upon returning from Canada to the United States no collections were attempted along the west side of the Bay of Fundy although the general physiography of that region was observed. Previously, unsuccessful collecting trips had been made to find cyathuras on Mt. Desert Island, Maine. That island with its hanging falls, rocky shore, high tides, and streams which disappear into boulder strewn beaches is, indeed, complex, but further north not only do these conditions exist but also one encounters dams, locks, and even reversing falls; it would appear, therefore, that because of their complexity, northern Maine and the Bay of Fundy region should be the subject for a separate study.

The United States National Museum has specimens classified as *Cyathura carinata* (Krøyer) from the following locations along the Gulf and Atlantic coastal states:

Lake Ponchartrain, Louisiana
Punta Rassa, Florida
Frankfort Bank, Key West, Fla.
Friend Key Lake, Fla.
Lake Poinsett, Fla.
Ogeechee River, Ga.
Edisto River, S. C.
Cooper River, S. C.
Winyah Bay, S. C.
Beaufort, N. C.
Potomac River, Va.
Chesapeake Beach, Md.
Chester River, Kent Co., Md.
Haverstraw, Hudson River, N. Y.
Beacon, Hudson River, N. Y.
Noank Harbor, Conn. (Aug. 28, 1874)
East Providence, R. I.

Vineyard Sound, Mass.
Davenport, Mass.
Rowley, Mass.

Specimens are lacking from 7 states: Texas, Mississippi, Alabama, Delaware, New Jersey, New Hampshire, or Maine. During the past 3 years, cyathuras have been taken in the last 4 states and additional collections have been made in states where they were already known. Extensive work has been done on the distribution and ecology of the cyathuras of Cape Cod, Mass. and this will be reported elsewhere. Following is a list of locations where the author and his friends have collected cyathuras along the coast of the U. S.:

Buckhorn Creek, Fla., 1½ miles from the entrance into Sopchoppy R.
Suwannee River, Fla. in vicinity of the town of Suwannee.
Lake George, St. John's River, Fla. (Three locations)
Sapelo Island, Georgia. (Dr. Alfred Smalley, collector)
Ashepoo River, S. C. where U. S. Route 17 crosses.
Calico Creek, N. C. (Near Beaufort)
Appoquinimink Creek, Del. under bridge on U. S. 13 north of Odessa.
Wading River, N. J. by state road 542.
Cape Cod and the Islands, Mass. (Cyathuras taken in 38 locations)
Smelt Brook, Rocky Nook, Mass. where R. R. crosses brook.
Branch of North River near Marshfield Hills, Mass.
Branch of "The Gull" by Hollet St., N. Scituate, Mass.
Weir River by state road 3A near Nantasket Jct., Mass.
Little River, Mass. along state road 121 in West Gloucester.
Exeter River, N. H. along state road 108.
Cider Hill Creek, Me., a tributary of the York River.
Chewonki Creek, Me., a tributary of the Sheepscot River. (Collected by Mr. Robert Hanks and the author.)

The North American isopod, *Cyathura* sp., is fully as large (27 mm) as any other described for the genus. Like most other anthurid isopods it bears a pair of statocysts in its tail. On the basis of laboratory and field observations and examinations of the contents of its alimentary tract, *Cyathura* sp., appears to be a detritus-algal feeder although it has chewing mouth parts (Menzies 1951) and we have seen it attack and partially eat gammarids. We have also seen it eat macerated tissue of dead elvers, dead *Crago* sp., abdominal area and intestine of small dead fish, and finally dead of its own kind. It in turn is known to be eaten by black duck, winter flounder, four-spine stickleback, and sea-run trout. Also, New Jersey fishermen report that cyathuras are eaten by the white perch, and, on Cape Cod, wading birds such as sandpipers, herons, and bitterns feed on flats where cyathuras live in large numbers.

In some 60 estuaries and tidal marshes where cyathuras have been found, the following conditions have been found consistently and are thought to be typical of their habitat niche:

1. *Cyathura* sp. live only where fresh and salt water mix.
2. The water covering the substrate where they live is never quiet for any appreciable length of time but is constantly in motion related to the slope of the land, tide, or wave action.
3. They live in simple unlined tubes of their own construction, although it is possible that they may use worm burrows as well.
4. Their substrate contains much or little sand with an admixture of vegetable debris, and at times, particularly in N. H. and Maine, blue clay.

Not always, but often, cyathuras are found, when following a water course from its mouth, at a point in the water where the cattail, *Typha,* succeeds the salt grass, *Spartina,* on the banks.

With one possible exception, *Cyathura sp.* seem to live in water of lower salinity in the south than they do in the north. In Lake George which is about 120 miles from the mouth of the St. John's River, Florida, cyathuras live continuously in water having a salinity of about 1 $^0/_{00}$. Elsewhere, north of Florida, water where cyathuras live reaches salinities as low as this at low tide. However, in Chewonki Creek in central Maine, even at dead low tide (see Fig. 6) the salinity was 17.3 $^0/_{00}$. The exception to the generalization first stated may be Frankfort Bank, Key West, Florida, for, unless springs of fresh water upwell as they do in coastal waters off St. Augustine, Fla., cyathuras at Frankfort Bank may live continuously in water having a salinity of over 30 $^0/_{00}$. However, since the author does not have first-hand knowledge of this area, the suggestion that this case is an exception to a south-north salinity gradient is only surmise.

Since both our field and laboratory observations show that adult *Cyathura* sp. can withstand both rapid changes and wide variations in salinity, it is not surprising to find a few individuals in bays or mouths of rivers at depths of several meters and in water of fairly high salinity, but in no case in our experience did these animals represent breeding populations. Such populations are found far upstream, often mingling with caddis-fly larvae damsel-fly, and may-fly nymphs, and on several occasions they have been found above the lower ranges of leeches living in tidal streams!

During the past several years we have worked almost entirely in the brackish water ecotone collecting a total of several thousand cyathuras and never in our experience have we found a locality represented by a single specimen. In general, along the eastern coast of the U. S., concentrations run from 100-200 individuals per m^2, but on Cape Cod they run much higher, and in one particular place, Pocasset River, which is the site of a special study, cyathuras are regularly found in densities of 1000-1500 m^2 with spring aggregations of nearly 4000! Apparently, the east coast North American cyathuras live in greater densities than those in England and Europe, for Spooner and Moore (1940) reported concentrations of 200 m^2 as unusual. Although he gave no quantitative estimates for cyathuras living in continental waters, Holthuis (Beaufort 1954) reported that *C. carinata* (K.) reached a maximum density in the Zuiderzee between 1932-39 after its closure when inflowing streams freshened it, and that in 1939, when it became almost completely fresh, the cyathuras disappeared.

When we first came in contact with the North American *Cyathura* sp. (Burbanck, Pierce, & Whiteley 1956) we were unaware of the global distribution of species in the genus and we had no idea that cyathuras were so plentiful. We are now convinced that, in some places along our eastern coast at least, they are an important link in the food-chain and, in any event, fascinating material for ecological, physiological, zoögeographical, and cytogenetic research.

Notes on *Cyathura* sp. from five locations along our eastern coast:

Salt Springs runoff. On June 23, 1956, *Cyathura* sp. was found in fine white sand in association with the clam, *Mulinia* sp., and gammarids. Damsel-fly nymphs and the mosquito fish, *Gambusia,* were in the immediate vicinity. At this time of year, female cyathuras carried eggs or young in their marsupia. The picture (Figure 2) was

FIG. 2. Runoff of Salt Springs, Fla. on June 23, 1956.

taken about mid-way between the spring and the point where the runoff enters Lake George. This is approximately 120 miles from the mouth of the St. John's River near Jacksonville, Florida. Where the cyathuras were found, there is little if any tide, but boats with outboards moving in and out of the spring cause a good deal of wave action. Just below the point where the spade is thrust into the sand the cyathuras were taken, and Mr. Billy Mitchell, through whose cooperation the trip was possible, is shown picking cyathuras and associated forms from the sieve used in separating the animals from the sand.

Ashepoo River, S. C. On July 13, 1956 where U. S. Route 17 crosses the river, cyathuras were taken in the

FIG. 3. Half tide on Ashepoo River, S. C. July 13, 1956. Shell-sand ramp in foreground where cyathuras were found.

submerged end of a hard shell-sand ramp used for launching boats from trailers (Figure 3). Associated with the isopods were nereid worms, blue crabs, and small barnacles. At this point the tide rose about 4 feet and the mouth of the river is about 25 miles to the southeast.

Calico Creek, N. C. On April 21, 1956, Dr. Carter Broad accompanied the author to the head of the creek where water flowed from a cattail, *Typha*, marsh. In a very restricted area around the old foot-bridge pilings (Figure 4) in a substrate of shell, broken glass, and sand the

FIG. 4. *Cyathura* sp. taken among pilings amid sand, shell, and broken glass in Calico Creek, N. C. April 21, 1956.

cyathuras were found. One female had eggs or young in her marsupium. No other animals were found associated with the cyathuras, and at this point about 6 miles from the mouth, the rise in tide was almost 3 feet.

Wading River, N. C. On December 28, 1957 when the air temperature was 5° C. and the substrate 2.5° C., 20 mm cyathuras were collected in a sand bar at a point where the bridge elevator reflected in the water (Figure 5). At this season, no females had marsupia and in

FIG. 5. Rising tide in Wading River, N. J., December 28, 1957.

the mucky clay closer to shore, juvenile forms of 8-10 mm were found. The only other animals living with the cyathuras were a few small nereids. Mrs. Alice Weber, who lives adjacent to the area shown in Figure 5, said that blue crabs came up the river during the summer and herring and perch in the spring. The latter, she said, ate the cyathuras. The tide at this point rises 4 to 5

feet and the distance from the mouth is about 12 miles. *Chewonki Creek, Maine.* On September 21, 1957, the author accompanied by Mr. Robert W. Hanks, Fishery Research Biologist for Clam Investigations at Boothbay Harbor, Me., went to Chewonki Creek where the latter had collected cyathuras on April 24 of the previous spring. Working at a dead low tide in September, cyathuras of maximum size (26-27 mm) were collected at a point (Figure 6) a little over a mile from the

FIG. 6. Chewonki Creek, Me. on September 21, 1957 at dead low tide. Cyathuras taken in gritty blue clay in small channel near island.

mouth of the creek where the tide rises 9-10 feet. The isopods were in a soft muck clay in which one sank at least 6 inches at every step. There was very little sand in this substrate, but a gritty texture could be felt when the clay was rubbed between the fingers. As previously noted, the salinity of the water at low tide was 17.3‰, and the marine algae, *Enteromorpha* and *Fucus*, grew attached to rocks adjacent to where the cyathuras were taken. Also, associated with the isopods were numerous clams, *Mya arenaria* and *Macoma baltica*, and nereid worms, *Neanthes virens* and *Nereis diversicolor*. There were also a few worms, *Glycera* sp., and the shrimp, *Crago* sp.

REFERENCES

Allee, W. C. 1923. Studies in marine ecology. I. The distribution of common littoral invertebrates of the Woods Hole region. Biol. Bull. **44**: 167-191.

Barnard, K. H. 1925. A revision of the family Anthuridae (Crustacea Isopoda) with remarks on certain morphological peculiarities. Jour. Linn. Soc. Zool. **36**: 109-160.

Beaufort, L. F. De. 1954. Veranderingen in de flora en fauna van de Zuiderzee (thans Ijesselmeer) na de afsluiting in 1932 (Verslag, Zuiderzee-commissie der Nederlandse Dierkundige Vereniging). De Helder, C. de Boer, Jr. (L. B. Holthuis XIV Crustacea Isopoda. 205-212).

Bousfield, E. L. 1955. Studies on the shore fauna of the St. Lawrence Estuary and Gaspe Coast. Bull. Nat. Mus. Canada. **136**: 95-101.

Burbanck, W. D., Madelene E. Pierce, and G. C. Whiteley, Jr. 1956. A study of the bottom fauna of Rand's Harbor, Massachusetts: An application of the ecotone concept. Ecol. Monog. **26**: 213-243.

Cooper, W. Omer. 1916. On some undescribed features in the structure of *Cyathura carinata* (Krøyer). Jour. Zool. Res. **1**: 97-101.

Day, J. H., N. A. H. Millard, and A. D. Harrison. 1952. The ecology of South African estuaries. Part III. Knysa: A clear open estuary Trans. Roy. Soc. So. Afr. **33**: 367-413.

De Kay, J. E. 1843. Zoology of New York. Albany: Carroll and Cook. Part V. 1-70.

Ganong, W. F. 1890. Southern invertebrates on the shores of Acadia. Trans. Roy. Soc. of Canada. **8**: 167-185.

Gould, A. A. 1841. Report on the Invertebrata of Massachusetts. Cambridge: Folsom, Wells, & Thurston.

Gurjanova, E. F. 1936. Isopodes des mers orientales. Faune de l'URSS. Nouvelle Série No. 6. **7**: 1-278.

Harger, O. 1878. Report on the marine Isopoda of New England and adjacent waters. U. S. Comm. Fish & Fisheries Rept. Part. VI.

———. 1879. Notes on New England Isopoda. Proc. U. S. Natl. Mus. **2**: 157-165.

Löwegren, Yngve. 1937. Sin fur die fauna Schwedens neuer Isopoder *Eurydice pulchra* Leach, sowie ein neues lokal für den Isopoder *Cyathura carinata* (Krøyer). K. Fysiogr. Sällsk Lund Förh. **7**: 182-185.

Lundström, A. 1937. Neue fondorte für *Cyathura carinata* (Krøyer) und *Polydora ligni* Webster. Ibid. 172-174.

Menzies, R. J. 1951. New marine isopods, chiefly from northern California, with notes on related forms. Proc. of U. S. Natl. Mus. **101**: 105-156.

Monod, Th. 1925. Tanaidacés et isopodes aquatiques de l'Afrique occidentale et septentrionale. Bull. Soc. Sc. Nat. Maroc. **5**: 61-84, 233-246.

Norman, A. M. and T. R. R. Stebbing. 1886. On the Crustacea Isopoda of the "Lightning," "Porcupine," and "Valorous" expeditions. Trans. Zool. Soc. Lond. **12**: 77-141.

Richardson, Harriet. 1905. Isopods of North America. Bull. U. S. Natl. Mus. **54**: 1-721.

Stammer, H. J. 1932. Die fauna des Timavo. Zool. Jahrb., Abt. Syst. Ökol. Geogr. Tier. **63**: 521-656.

Spooner, G. M. and H. B. Moore. 1940. The ecology of the Tamar Estuary. VI. An account of the macrofauna of the intertidal muds. Jour. Mar. Biol. Assoc. **24**: 283-330.

Stephensen, K. 1948. Storkrebs IV. Ringkrebs 3. Tanglus (Marine Isopoder) og Tanaider. Dansmarks Fauna. **53**: 1-187.

Stimpson, W. 1855. Descriptions of some new marine Invertebrata. Proc. Acad. Nat. Sci. Phila. **7**: 385-394.

Tattersall, W. M. 1922. Zoological results of a tour in the far east. Amphipoda with notes on an additional species of Isopoda. Mem. Asiatic Soc. Bengal. **6**: 435-459.

Verrill, A. E. and S. I. Smith. 1874. Report upon the invertebrate animals of Vineyard Sound and adjacent waters. U. S. Comm. Fish & Fisheries Rept. 1871-1872: 295-852.

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EFFECT OF VISIBLE LIGHT ON THE GROWTH OF *TETRAHYMENA PYRIFORMIS*[1]

Introduction

In the literature on the growth of protozoans, numerous references have been made to the desirability of raising laboratory cultures in a "north window" or under subdued light. That they usually die if exposed to strong sunlight is well known, but the reason for this phenomenon has not been satisfactorily explained.

Maupas (1888), using *Stylonychia* in his experiments, showed that during the summer months the growth rate of the oganism was greater than during the winter, and suggested that this was probably due to the temperature differential, rather than to difference in the amount of light. Richards (1929), using the ciliates *Paramecium, Histrio,* and *Blepharisma,* made the same observation, but attributed the more rapid growth during the summer months to the greater amount of visible light per day. No temperature control was used in this work.

The present paper shows that in the case of 2 strains of the ciliate, *Tetrahymena pyriformis,* the growth of organisms in medium which has been subjected to strong light, such as that of the sun, is greatly impaired. Further investigation indicates that this phenomenon is due solely to the destruction of riboflavin by visible light. That this vitamin is converted into either lumiflavin (in alkaline solutions) or lumichrome (in neutral or acid solutions) is well known (Kuhn *et al.* 1934). In as much as *Tetrahymena* is dependent upon an exogenous source of riboflavin (Kidder and Dewey 1949), the question arises as to how these protozoans are able to survive in nature, where they are periodically exposed to riboflavin-destroying sunlight. The results of work undertaken to answer this question show that through the assimilation of riboflavin obtained from riboflavin-producing bacteria, *Tetrahymena* can maintain its supply of this vitamin. Some of these findings have been published in an abstract, Phelps (1949).

Materials and Methods

The oganisms used in this work were *Tetrahymena pyriformis,* strains "W" and "HS," Corliss (1953), raised axenically (bacteria-free) in 0.5% proteose peptone and tap water. Rates of growth were determined by direct count, using the Sedgwick-Rafter counting chamber. Details of exposure to light will be given in the description of each experiment.

Experiment 1. Twenty-five ml of culture medium were placed in each of two 50 ml Florence flasks, and were inoculated with approximately 250 organisms per ml of strain "W," which was in the exponential growth phase. Both flasks were stoppered, and one, the control, was covered with tin foil. Both were immersed to a depth of 75 cm in a pond of clear water in order to rule out the effect of U.V. radiation. They were left for 6 hours. The temperature in situ was 24°, and the light intensity, as determined by a calibrated photoelectric cell, varied from 3500 to 5000 foot candles. At the end of the experiment it was found that the organisms in the exposed flask were immotile, and they subsequently disintegrated, while those in the protected flask showed normal growth.

Experiment 2. Similar flasks containing approximately 2500 organisms per ml of strain "W" in the exponential growth phase were exposed to sunlight filtered through 220 cm of clear pond water for 5 hours at a temperature of 22°. This experiment was repeated twice. The average light intensity was 200 foot candles. Diminution of growth in the exposed flasks as opposed to that in the protected flasks is shown in Table I.

Table I. Growth in protected flasks *vs.* light exposed flasks at a depth of 220 cm of water and an average light intensity of 200 foot candles

Protected Flasks		Exposed Flasks	
Initial Count	Count after 5 hours	Initial Count	Count after 5 hours
2430	4617	2412	4313
2374	4973	2355	3562
2636	4860	2486	4212
Av. 2480	4817	2418	4029
P. E. 95.5	122	44	264

Experiment 3. Uninoculated medium at room temperature was placed in culture tubes and exposed to a 1000 watt incandescent bulb which was immersed in a bowl of flowing cold water. This gave an illumination of 2000 foot candles at the site of the medium. One of the tubes was protected by tin foil. After an exposure of 8 hours, both tubes were placed in the dark at 18°, and were inoculated with approximately 100 organisms per ml. As is seen Figure 1, the control, which was

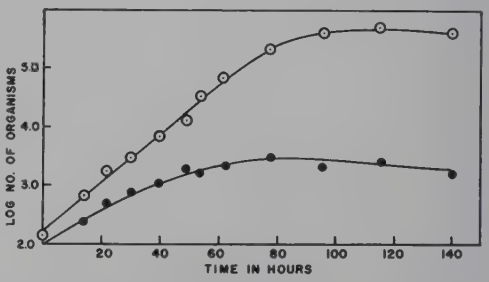

Fig. 1. Growth in light-exposed medium shown by solid circles. Growth in medium protected from light shown by open circles.

medium that had been protected from light, had an average division time of 6.5 hours, and achieved a maximum population of 330,000 per ml whereas the test medium had a division time of approximately 14 hours, and went to a maximum of only 3100 per ml. This experiment was repeated with strain "HS" and the results were essentially the same.

Experiment 4. Culture medium was exposed as in experiment 3, and to the exposed tubes the following vitamins were added (concentrations expressed as μg/ml).

Thiamin	1.0
Calcium pantothenate	0.1
Pyridoxine	2.0
Niacin	0.1
Riboflavin	0.1
Folic Acid	0.01
Biotin	0.0005

[1] This work was assisted by funds from the Research Institute of The University of Texas.

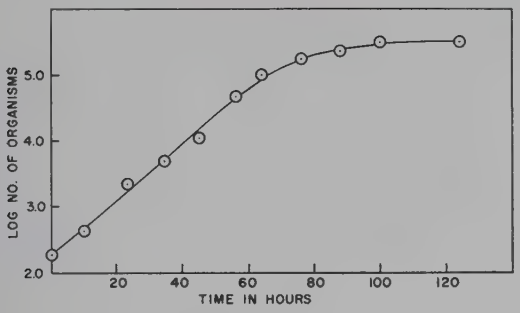

FIG. 2. Growth on light exposed medium to which 7 vitamins have been added.

Figure 2 shows that the growth of strain "W" was essentially the same in the light exposed vitamin-enriched medium as in the control, shown in Figure 1.

Experiment 5. After testing different portions of the above vitamin complex, it was found that riboflavin, and riboflavin only, restores light-exposed medium to its original potentiality. In Figure 3 is shown growth in exposed medium to which 0.1 μg/ml of riboflavin, and no vitamins, had been added.

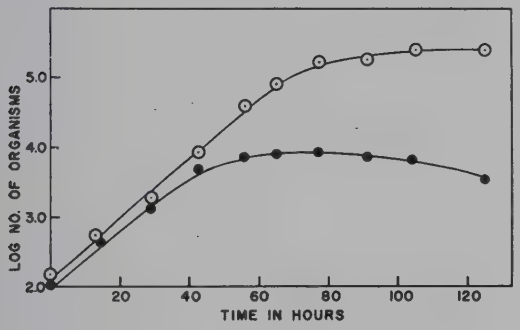

FIG. 3. Growth in light-exposed medium shown by solid circles. Growth in light-exposed medium to which riboflavin had been added shown by open circles.

Experiments 1 through 5 have established the fact that exposure of medium to visible light inhibits normal growth of *Tetrahymena*. Since visible light destroys riboflavin, and since the nutritive quality of light-exposed medium is restored by the addition of this vitamin, it is concluded that this inhibition is due to destruction of riboflavin.

The following experiments were undertaken to discover how under these conditions the organisms can survive in nature. It seems possible that they obtain riboflavin from those bacteria which continuously synthesize this vitamin. Experiment 6 was designed to test this theory:

Experiment 6. *Tetrahymena* (strain "W") was inoculated into 2 tubes of medium which had been exposed to strong light. To one of the tubes was added living *B. subtilis*. Heavy growth of the protozoans occurred in the tube containing the bacteria, but not in the control tube.

In order to establish that factors other than riboflavin were not involved, the following experiment was performed:

Experiment 7. Tubes of proteose peptone medium which had been exposed to strong light were inoculated with *Lactobacillus caseii*, which produces riboflavin. Other tubes, similarly exposed, were inoculated with *L. arabinosus*, which cannot produce riboflavin, and is dependent upon exogenous sources for it. After light growth of the bacteria had occurred, all tubes were autoclaved and then inoculated with *T. pyriformis* strain "W." Growth of the protozoa was normal in medium which contained *L. caseii*, but was poor in medium which contained *L. arabinosus*.

From these experiments it is concluded that *Tetrahymena* obtains its riboflavin from the riboflavin-producing bacteria in its immediate environment, either by absorbing the vitamin which has diffused into the water, or by eating the bacterial cells. It is reasonable to assume that this method of obtaining riboflavin in nature is used by all protozoans that live in natural waters, and that require an exogenous source of riboflavin.

SUMMARY

1. Exposure of proteose peptone medium to strong light in the visible spectrum renders it unsuitable for growth of the ciliate, *Tetrahymena pyriformis*.

2. Addition of 6 vitamins does not restore the ability of light-exposed medium to maintain normal growth, but addition of riboflavin alone restores it completely. This indicates that photic destruction of riboflavin is responsible for the effect.

3. Normal growth of *Tetrahymena* in light-exposed medium is restored by the presence of riboflavin-producing bacteria.

REFERENCES

Corliss, J. O. 1953. Comparative studies on holotrichous ciliates in the *Colpidium-Glaucoma-Leucophrys-Tetrahymena* group. *Parasitology* **43**: 49-87.

Kidder, G. W., and Virginia C. Dewey. 1949. Studies on the biochemistry of *Tetrahymena*. XIII. B vitamin requirements. Arch. Biochem. **21**: 66-73.

Kuhn, R., T. Wagner-Jauregg, and H. Kaltschmitt. 1934. Über die Verbreitung der Flavin in Fflanzenreich. Ber. Deut. Chem. Ges. **67**: 1452-1457.

Maupas, E. 1888. Recherches expérimentales sur la multiplication des infusoires ciliés. Arch Zool. Exp. Gen. (ser. 2) **6**: 165-277.

Phelps, A. 1949. Effect of visible light on the growth of *Tetrahymena geleii*. Anat. Rec. **105**: 500-501.

Richards, O. 1929. The correlation of the amount of sunlight with the division rates of ciliates. Biol. Bull. **56**: 298-305.

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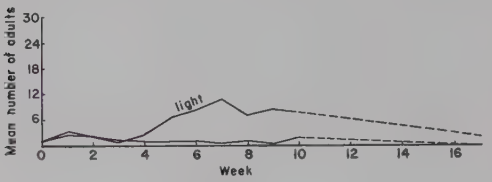
SIMOCEPHALUS REPRODUCTION AND ILLUMINATION[1]

Stephens (1952) has shown that ovarian development in *Cambarus* is partially controlled by photoperiod. Subsequent work by Stephens (1955) suggested that molting of this crustacean is also influenced by duration of photoperiod. *Simocephalus vetulus,* a common cladoceran, has been used in analyzing competition between it and the copepod *Cyclops viridis* (Parker, unpublished). Since the young of *Simocephalus* are released shortly before molting, results with the above mentioned crayfish prompted an experiment which compared *Simocephalus* population growth under continuous lighting and in complete darkness for a period of 10 weeks. Individual cultures were started with one gravid female in 50 ml of pond water which had been filtered through number 25 silk bolting cloth, and 10 cultures were maintained at 20° C at each photoperiodic extreme. Animals were enumerated weekly according to 2 arbitrary size-age categories (juveniles and adults), placed in fresh medium, and supplied with a one ml suspension of *Chlamydomonas moewusii* having a Klett photometer density of 75 under a red filter.



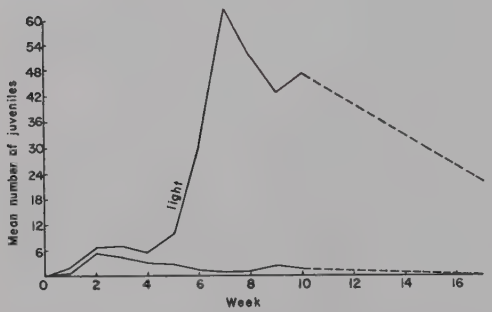


FIG. 1. Weekly variation in the mean number of *Simocephalus* adults per culture under continuous fluorescent illumination and in complete darkness.

FIG. 2. Weekly variation in the mean number of *Simocephalus* juveniles per culture under continuous fluorescent illumination and in complete darkness.

[1] This investigation was supported in part by a research grant RG-5241 from the National Institutes of Health, Public Health Service. The assistance of Mrs. Rosana Brousseau is gratefully acknowledged.

Figure 1 shows the fluctuation in mean number of adults per culture over the course of the experiment. It is apparent that no difference exists between the culture types until after week 3 when the lighted populations reach numbers 2 to 10 times as high as populations kept in the dark. Of greater significance are the figures for juvenile numbers as illustrated in Figure 2. The positive effect of light on reproductive rate is evident from the beginning of the 10-week period, and is most prominent at week 7 when the mean is about 60 times as large.

Of additional interest is the failure of some dark cultures to maintain themselves for the entire 10 weeks. Two of these reached zero by the eighth week and 2 more by the ninth week. Following the completion of the designated period all cultures were kept without water changes and food for seven more weeks. At the end of this time, all members of the dark cultures were dead in contrast with all light cultures where adults still averaged 2.4 animals per container and juveniles 22.2 animals per container.

References

Stephens, Gwen J. 1952. Mechanisms regulating the reproductive cycle in the crayfish, *Cambarus.* I. the female cycle. Physiol. Zool. **25:** 70-84.

Stephens, Grover C. 1955. Induction of molting in the crayfish, *Cambarus,* by modification of daily photoperiod. Biol. Bull. **108:** 235-241.

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SURVIVAL OF BRANCHIOBDELLID ANNELIDS WITHOUT A CRAWFISH HOST

Branchiobdellids were regarded as obligate ectoparasites of crawfishes until Goodnight (1940) showed that their food consisted of diatoms and suggested that they were not parasitic but commensal in habit. All species described to date have been found only on the external surfaces of crawfishes, leading to the generally accepted conclusion that these small leech-like oligochaetes cannot survive without crawfish on which to live.

In an aquarium in one of the laboratories here an isolated specimen of the crawfish *Procambarus clarki* died and remained unnoticed for several days. When this individual was noticed it was in an advanced state of decomposition and its entire surface was covered with an estimated 200 branchiobdellids. These were all attached posteriorly, but actively moving their free head ends. Three were removed to a watch glass with some of the polluted water for identification. Through carelessness the watch glass was not washed immediately following the original observation. The following day the worms were found alive and quite active. A cover was placed on the watch glass and daily observations made thereafter. At the outset the water supported a thriving colony of paramecia and was covered by a thin layer of scum. At the end of the first week one of the worms had disappeared and other 2 were active, but the water had evaporated, leaving only a film of scum. Water was added as needed and the worms seemed to thrive well as long as there were paramecia present, although on no oc-

casion was there any indication that the protozoans served as a food supply. All paramecia were gone by the end of the third week. The 2 worms were still active and apparently in good condition (though probably starved) at the end of 2 months (July 18 to September 18) when they were killed. Professor Clarence J. Goodnight of Purdue University identified them as *Cambarincola vitrea* Ellis.

Although these observations support the possibility of a free-living existence for branchiobdellids, the writer believes that any free-living existence under natural conditions would be merely of duration long enough to allow for transfer to a new crawfish, or to the same crawfish following molting.

Reference

Goodnight, C. J. 1940. The Branchiobdellidae (Oligochaeta) of North American crayfishes. Illinois Biol. Monogr., **17**: 1-75.

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NOTES ON THE LIFE HABITS AND POTENCY OF THE VENOM OF THE THREE *LATRODECTUS* SPIDER SPECIES OF ISRAEL[1]

Occurrence

Three species of *Latrodectus* (Black Widow) spiders are known from Israel, as follows:

(1) *L. tredecimguttatus* P. Rossi 1790 is known from the Mediterranean area, Central Asia, South Russia and the Caucasus, Canary Islands, Ethiopia, Saudi Arabia, St. Helena (Reimoser 1919, Roewer 1942). In Israel the spider is found in the hilly areas, the coastal plain, the Jezreel and Jordan Valleys, Haifa Bay and near Beersheba and Kurnab.

(2) *L. pallidus* Cambr. 1872 was originally described from Palestine and later recorded also from Syria, Egypt, Tripolitania and the Persian Gulf. In Israel it occurs in the Jordan and Jezreel Valleys, near Tel Aviv, and in the area around Beersheba and southward for a distance of some 60 km.

(3) *L. revivensis* Shulov 1948 is so far known only from its Israel home at Beersheba and the area to the south for a distance of some 40 km, particularly around the settlement of Revivim (Shulov 1948).

The three species are readily differentiated on the basis of the coloration of the young, the form of the bristles on the dorsal side of the female, and the structure of the web (Shulov 1948).

Abundance

As many as 150 adult and sub-adult specimens of the 3 local species of *Latrodectus* have been found during a single excursion to the Beersheba area, 2 of which were made on 15.V.55 and 3.VII.55, while the collection of additional material in the same area during 2 other trips 3 years later, in October, 1958, provided more than enough individuals to permit a detailed comparison of the characteristics and behavior of the 3 species.

In one plot of about one acre in area it was possible to collect 20 adult females of the 3 species, together with their egg cocoons, as well as a number of males. The presence of 3 species of *Latrodectus* on a single small plot of land would seem to be unusual, although mass occurrences of *Latrodectus tredecimguttatus* have been reported from Europe, Asiatic Russia and the Balkan peninsula (Pavlovsky 1927), while numerous descriptions have been given of the mass occurrence of *L. mactans* Fabr. in North and South America (Blair 1934, Herms *et al.* 1935) and of *L. geometricus* Koch in the Philippines (Keegan *et al.* 1950). In addition it is known that the distributional area of a number of species is slowly expanding, because of the increased ramification of man-made means of communication and transport, whereby species are introduced into new areas and settle permanently in the proximity of endemic species. Reports of such infiltration by *L. hasselti* Thorell and *L. geometricus* Koch have been given by Keegan (1952). In the Beersheba area, the occurrence together of the 3 local species of *Latrodectus* would seem to have resulted from the considerably increased vehicular traffic through the town in the past few years.

Web Structure

While 2 species were found in a number of places to have constructed their webs on or in the same object, such as an electric-line pole, shrub, ditch, abandoned rodents' nest or empty preserve tin, the webs of the 3 species differed conspicuously with regard to their height above ground level, the shape of the funnel, the outline of the retreat, the type of corridor and bridge and the variety of food remnants clinging to the threads (Figure 1).

L. tredecimguttatus constructs its web at the level of the ground, concealing the major part of it within crevices in the soil or beneath large stones, at the base of shrubs, in rodent holes and in tin cans lying on the earth. In contrast, the web of *L. revivensis* is usually constructed at a height of 35-40 cm above ground level and that of *L. pallidus* at a height of some 40-60 cm, invariably affixed to the leaves and branches of low shrubs or other vegetation.

With regard to the retreat, the structure is of a clearly-outlined thimble-shape in the case of *L. pallidus*, which spins it from a white, thin and opaque material (Figure 2, Figure 3). In contrast, the retreat of *L. revivensis* is conical to cylindrical in form, is shallower than that of *L. pallidus* and is located upon the upper side of the funnel, although not always on the narrowest part of the latter (Figure 4, Figure 5). The web of *L. tredecimguttatus* contains no regularly outlined retreat, its function being formed by an invagination of the funnel, sometimes at its highest and sometimes at its deepest point. Nor does the funnel of the web of *L. tredecimguttatus* display a regular outline, in contrast to that of *L. revivensis*, which is short and broad and generally constructed so as to lie in a horizontal position (Figure 6) and to that of *L. pallidus*, which is bent in the form of a chemical

[1] Grateful acknowledgment is made to Mr. P. Amitai for his skillful technical help.

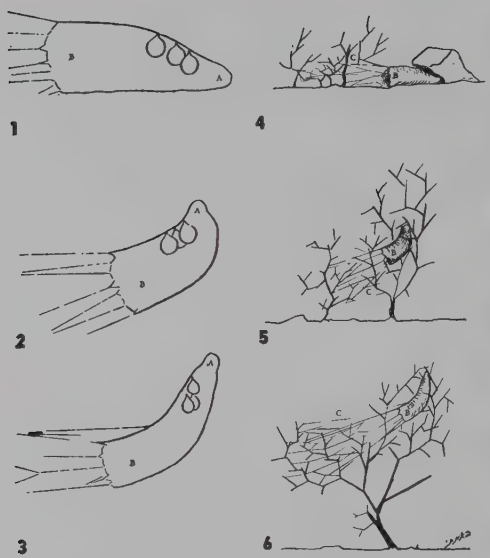

FIG. 1. Semi-diagramatic representation of the 3 types of webs of *Latrodectus* and their position in relation to the ground.

1. Web of *L. tredecimguttatus,* retreat (a) slightly differentiated and situated at the end of the horizontal funnel (b).

2. Web of *L. revivensis,* retreat (a) above the broad and slightly curved funnel (b), and distinctly differentiated.

3. Web of *L. pallidus,* retreat (a) situated at the upper end of the funnel (b), which is narrow, elongated and curved.

4-6: Drawn from typical webs in the fields, these figures show the differences in location of the web in relation to the ground.

4. *L. tredecimguttatus* funnel almost completely concealed in a recess in the ground.

5. *L. revivensis* web situated 40 cm above ground level, the corridor threads (c) inclined downwards.

6. *L. pallidus* web situation, 60 cm above ground level, the corridor (c) chiefly horizontal in position.

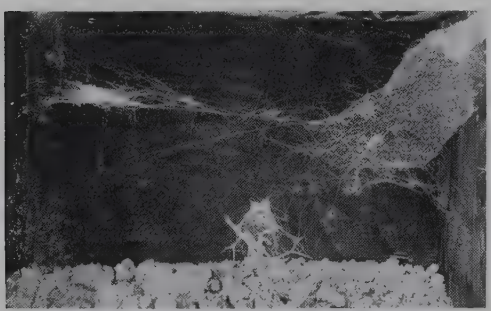

FIG. 2. Web of *L. pallidus* spun in a box in the laboratory. The retreat and the funnel (right upper corner) are clearly seen. On the left side of the photo is situated the center of the bridge, connected with the funnel. The external threads of the corridor are seen in the middle.

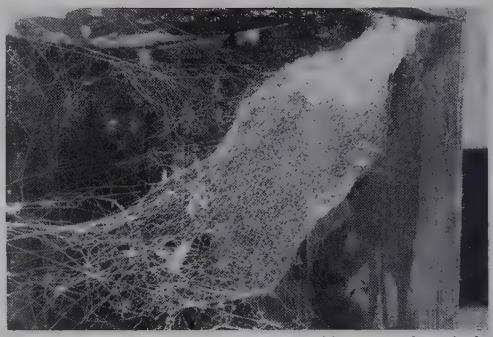

FIG. 3. The same web enlarged. Note the threads in the upper left corner, which support the funnel and the corridor (left lower corner).

FIG. 4. Web of *L. tredecimguttatus* on the ground within a hollow or recess lying under the shelter of an overhanging mass of soil. The retreat (left center) and the funnel are covered by blades of grass and dried bits of plants. The corridor (rising to the right) consists of a few threads of web material only.

retort rising vertically into the air, with a round entrance hole at the lower end. Of the 3, the funnel of *L. pallidus* is the thinnest and most transparent.

The corridor of the *L. pallidus* web is spun from individual threads in the form of a large cylindrical tube tapering in the direction of the retort-shaped funnel. The web in this species also possesses a well-developed triangular bridge over ants' trails (Shulov 1940), down which the spider descends to seize its prey. The species also spins a well-developed bridge of thick threads connecting adjacent shrubs. In *L. revivensis* there is rarely a well-developed corridor, although the threads may extend up to 95 cm in length, while a few thick threads sometimes serve as a bridge between two shrubs. The web of *L. tredecimguttatus* is without a pronounced corridor.

The remnants of food encased within the walls of the funnels of the webs of *L. revivensis* and *L. tredecimguttatus* consist of beetles, including Tenebrionidae, such as *Adesmia, Ocnera, Pimelia* and *Tentyria,* some Pyrrhocorid bugs (Heteroptera), and some *Messor* ants.

FIG. 5. Web of *L. tredecimguttatus* shown above after being laid open and the vegetation cleared away (enlarged x 2 in comparison to Fig. 4). Note the egg cocoon in the neck (opening of the retreat) and the female spider to the right of it. The thin stick lying at the bottom of the web indicates the level of the soil.

FIG. 6. Web of *L. revivensis,* surrounded in typical fashion by stems and branches of surrounding plants and shrubs. Two carcasses of beetles are seen interwoven into the walls of the funnel. Beetle at upper right is situated below the retreat. The corridor is situated to the left, below the funnel.

In 3 cases small scorpions and Isopoda have been found in the webs of *L. revivensis,* although scorpions have also been found in the webs of *L. tredecimguttatus* on other occasions (Shulov 1940). As indicated above, ants comprise the chief prey of *L. pallidus,* and remnants of ant bodies are found woven into the funnel. In addition to animal remains, the webs of *L. revivensis* and *L. tredecimguttatus* contain various objects such as pieces of wood, dry leaves, small stones and fragments of sheep droppings.

Egg Cocoons

The smallest egg cocoons are those of *L. pallidus.* Both the eggs and cocoons are clear white in this species. In the case of *L. tredecimguttatus,* the egg cocoons consist of white nearly globular sacs 14-17 mm in length and 12-15 mm in width, with one end pointed. The eggs themselves are orange-rose in color. The cocoons of *L. revivensis* are highly variable in shape and size. The color, like that of *L. tredecimguttatus,* is white, while the eggs are a light yellow-orange.

Color Variations

The young spiderlings of *L. tredecimguttatus* when leaving the cocoons are black with characteristic light spots, which gradually change in color from brownish-yellow to red. The *L. pallidus* spiderlings are pearly white, with 2 rows of yellow-brown markings. In the males, this coloration persists, but in the females from the IV instar onwards, the dorsal surface of the abdomen turns a uniform pearly-white or light brown-yellow in color, without markings, but with 6 small brownish-black punctations. In *L. revivensis,* the young spiders are colored like those of *L. pallidus* during the first 3 instars, and the males remain so colored, but the females assume a characteristic coloration from the fourth instar on in this species also, becoming dark brown or black, similar to *L. tredecimguttatus.* (See Shulov 1940, 1948 in regard to the color changes of *L. revivensis* during growth). *L. revivensis* thus in certain respects resembles *L. tredecimguttatus* and in others resembles *L. pallidus,* with regard to the color characteristics of the species.

Potency of Venom

An estimation of the potency of the venom of the three spider species arrived at by means of permitting serial bites to be delivered to white rats has been reported in previous papers (Shulov 1940, 1948). In the present investigations, additional data have been collected on the basis of injections of emulsions formed by macerating one pair of poison glands per 1 ml of saline, followed by decantation. White rats weighing 50 g were injected subcutaneously. The results are tabulated in Table I, expressed as the minimum volume of solution per g of rat required to cause death (minimum lethal dose). The findings indicate that the venoms of *L. tredecimguttatus*

TABLE I. Comparison of potency of venom of three Israel *Latrodectus* spider species

Species	No. of females used	No. of rats injected	M.L.D. cc/g
L. tredecimguttatus	21	20	0.004
L. revivensis	32	40	0.006
L. pallidus	38	30	0.022

and *L. revivensis* are similar in potency (MLD = 0.004-0.006 ml/g of white rat), while that of *L. pallidus* would seem to be considerably less potent than either of these (0.022 ml/g of white rat). However, estimations of potency based on minimum lethal dose methods at best provide only a rough approximation to the actual strength of venom, so that further investigations are needed employing more precise methods of venom standardization.

Conclusions

The results of the present investigation are of interest as regards the taxonomic and evolutionary position of the species peculiar to Israel, *L. revivensis*. The presence of 3 different species of *Latrodectus* in a single circumscribed area of ground, which provided an opportunity to make a comparison of how each selected the eco-niche and micro-ecological conditions to which it was genetically best fitted or adapted, showed that distinct differences occurred in the form and location of the web, and the specific food. Other distinct differences were noted in the type of coloration occurring in the egg and in the maturing spider at different stages of development, as well as in the potency of the venom of each of the 3 species.

References

Blair, A. W. 1934. Life History of *Latrodectus mactans*. Archives Inst. Med. **54**: 831-850.

Herms, W. B., S. F. Baily, and B. McIvor. 1935. The black widow spider. Univ. Calif. Coll. Agric., Agric. Exper. Sta. Bull. 591.

Keegan, H. L. 1952. Geographical distribution of *Latrodectus hasseltii*. Amer. J. Trop. Med. Hyg. **1**: 1073-1046.

———, **A. S. Blauw and R. J. Anderson.** 1950. *Latrodectus geometricus* on Luzon. Amer. J. Trop. Med. Hyg. **30**: 901-906.

Pavlovsky, E. N. 1927. Gifttiere und ihre Giftigkeit. Jena. G. Fisher.

Reimoser, E. 1919. Katalog der echten Spinnen (Aranea) des palaerktischen Gebietes. Abh. Zool. Botan. Ges. Wien 10, Heft. **2**: 280.

Roewer, C. F. 1942. Katalog der Sippen. Bremen.

Shulov, A. 1940. On biology of two Latrodectus spiders in Palestine. Proc. Linn. Soc. Lond. Sess. **152**: 309-328.

———. 1948. *Latrodectus revivensis* sp. nov. from Palestine. Ecology **29**: 209-215.

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REVIEWS

Ecological Genetics[1]

"Ecological genetics is a new integrating field in biology for which the principles have not been formally stated. Its objective is study of the hereditary structure that controls the mechanisms and processes through which ecological races and species have become adjusted to their environments." These opening words in the preface to the latest in the exhaustive monographs on "Experimental Studies on the Nature of Species" stand as both a beacon and a challenge to ecologists. The Carnegie Institution team of 'cyto-taxo-geneticist' (as Jens Clausen once dubbed himself) and plant physiologist have, ever since the pioneering work of Harvey Monroe Hall, underscored the significance of the genotype-environment interplay that molds plant populations to their habitats. For ecologists, the findings of the Carnegie botanists stand as warnings that genetically controlled ecotypic variation must be taken into account in both syn- and autecological studies.

The present volume of this continuing series (Part IV) entitled "Genetic Structure of Ecological Races" is the culmination of the painstaking, detailed approach that is required to delineate the genetics of ecotypic variation. The 312 pages are divided into four extensive chapters. Chapter I summarizes the genecological and taxonomic features of the chief experimental organism—the diploid, ecotypically variable *Potentilla glandulosa*. The account of ecological races in this species is a detailed summary of over two decades of experiment and observation. Some fine 'pearls' are cast before the student reading this chapter. For example, speaking of intraracial variability, the authors state: "Races tend to exhibit greater individual variability when grown in an environment near their threshold of tolerance than when they are grown in an environment to which they are well fitted. In an unfavorable climate, small differences between individuals may determine success or failure, whereas a race is likely to appear to be more homogeneous when it grows in an environment suited to all its individual variants." In summarizing the complexity of the *Potentilla glandulosa* population system it is pointed out that four levels of variability are detectable: (1) individual variation in the local population, (2) variation between isolated local populations, (3) regional differentiation in respect to climatic and edaphic differences which may or may not be discernable as morphologically distinguishable ecologic races, and (4) the taxonomic subspecies of *P. glandulosa*, readily distinguishable morphologically and ecologically. Given these levels of variability plus the reality of intergradation at and between successive levels, the species is revealed as a complex mosaic of continuous and discontinuous variation. All of which would add formidable overtones for one who attempts an ecological study of such a species.

Chapter II, "Genetics of Ecological Races" is an awesome compilation of the genetic analysis of artificial interracial hybrids through (in part) to the F_3 progeny. Segregating progenies of these hybrids were grown at Palo Alto and clonally at three altitudinal stations along an east-west transect from the High Sierra to sea-level at Palo Alto, California. Progeny were scored for physiological and morphological response. An instructive account is given of the handling of the masses of data by punched-card sorting techniques.

At this point, summary of the Carnegie study is dangerous; each of nineteen morphological and physiological traits is exhaustively analyzed, some of which would merit detailed discussion. Table 38 (p. 109) is a revealing synthesis of the genetic analysis. It lists the estimated number of genes governing the nineteen traits. Over 100 gene pairs regulate the expression of these traits. Although it is evident that phenotypes are under the control of "intricately balanced gene systems," by no means are they infinitely complex: "The inquiry indicates that the differences can be resolved in terms of a reasonable number of genes that is well within the range of experimental study." The chapter concludes with an analysis of genetic correlation—the degree of genetic linkage between pairs of characters. Two graphs (Figures 23 and 24) present the statistical correlations of character pairs. Both figures reveal that all degrees of correlation exist and that the magnitude of significant correlation differs markedly from one F_2 progeny to another.

While the genetic analysis of characters under uniform conditions attempts to resolve the nature of genotypic control in natural populations, still another facet of genetic structure demands analysis. "Basic to an understanding of genetics, and of the processes of natural selection, is knowledge concerning the phenotypic expression of genes and of gene combinations over a range of environments. This aspect of genetics has been explored but little." Thus in these terms, does Chapter III approach the genetics of natural populations, assessing "Response Patterns at Contrasting Altitudes." F_2 individuals were cloned and planted at the three transplant stations in California. It appears that environmental modification of phenotypic expression has its greatest influence on quantitative characters, while qualitative characters are only moderately affected in contrasting environments. Analysis of the genic control of the quantitative characters has proved difficult; indications are that such genic control yields a transgressive type of segregation whereby phenotype response is extended beyond the parental limits.

In summarizing Chapter III, Clausen and Hiesey reach the conclusion that ecological races show a well-defined coherence of the genetic structure that defines the race. Yet this coherence is flexible enough to allow extensive recombination, should selective pressures, migration, or confluence of racial borders change. Such a dynamic equilibrium is a potential source of evolutionary change.

Over one hundred pages of literature review and analysis follow in Chapter IV, entitled "Systems of Genes Controlling Characters and Their Significance in Environmental Adaptation and Evolution." Beginning with Bateson and Johannsen, the reader is presented a cavalcade of research on multiple factor inheritance followed by a review of significant studies on gene control of

[1] Clausen, Jens & William M. Hiesey. 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Washington, D. C.: Carnegie Institution of Washington Publication 615. vii + 312 pp., 68 tables and 33 figs. $4.25 paper, $4.75 cloth bound.

biochemical and physiological effects and their phenotypic variability in different environments.

A retrospective résumé of concepts regarding the genetic structure of ecological races is found in the short, last chapter. The nature of their investigation has limited the extent to which results are interpreted in the general area of genetics. The polygenic variations that factor pairs do exhibit, fall into categories of gene systems familiar to classical Mendelian genetics (e.g., epistasis, oppositional genes, multiple factors, etc.). What is significant is that the gene systems are claimed to be of "moderate complexity," analyzable, painstaking though it may be, by established genetic procedures. Thus, the authors state that in *Potentilla glandulosa*, a single qualitative character is controlled by from 3 to 6 gene pairs. That genetic control of variability can be thought of in such relatively simple terms is reassuring. But can we overlook the possibilities of other sources of genetic variability that are coming to be recognized in modern genetics—such phenomena as pseudoallelism, compound loci, multiple alleles, cytoplasmic inheritance, position effect, para-mutation, mitotic recombination, etc.? That this hiatus in their work exists, Clausen and Hiesey acknowledge. Theirs is a monumental contribution to even a partial understanding of the genetics of ecological races. It should serve as a model for similar genetic studies by other plant and animal biosystematists. Though the operational regimen for ecological genetics may not yet be well defined, this work will long remain a standard for comparison and emulation.

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Methods for Studying Communities of Terrestrial Animals[1]

A significant lack among recent ecology books in English has been specific descriptions of methods for estimating field populations of terrestrial animals. The final two thirds of Balogh's book provides this information in great detail. For anyone planning a field study, it is an invaluable compendium of techniques. Balogh himself has written the major part of the methods section—that pertaining to invertebrate populations under natural conditions. He has enlisted the help of several specialists in different taxonomic groups; and two of them, F. J. Turček of Czechoslovakia and B. Heydemann of Germany, have contributed chapters on methods for vertebrates and cultivated areas respectively.

It is Balogh's section that is really outstanding. After some twenty pages of general considerations, such as plans, choice of site, preliminary observations, and sources of error, he considers the methods from three standpoints: kind of sampling that can be done (quadrats, transects, traps, capture-release-recapture, etc.); stratum of the community to be sampled; and individual phylum to be collected. The methods are described and illustrated in sufficient detail so that no further search for procedure is necessary, although Balogh advises the reader to consult the original papers. Of exceptional value are the numerical data quoted liberally from the literature. These data provide guides to the numbers of organisms to be expected in various natural situations, and there are many comparisons between the numbers obtained by different methods, sometimes with the degree of statistical significance indicated.

The first third of the book is devoted to principles of community ecology, as exemplified in terrestrial situations. It is divided into sections on "General Biocoenology," "Production Biology," and "Analysis of Zoocoenoses." Although Balogh equates "Biocoenology" with ecology, it is apparent that his use of biocoenology is more restricted than the usual use of ecology, and that a literal translation comes nearer to the meaning. After a considerable discussion of the history of the term biocoenosis, he concludes that Möbius had in mind a concept about equal to that currently embodied in the term ecosystem. He prefers biocoenosis because of priority and also because ecosystem emphasizes the distinction between living and non-living elements—a separation that exists only in the mind.

The parts dealing with the description, subdivision, delimitation, and analysis of biocoenoses are revealing to the American ecologist in several ways. The most significant of these is the large number of papers published by Hungarian ecologists in the past few years. It is not possible to evaluate this work accurately on the basis of secondary information, but the impression gained from reading Balogh is that it is important and voluminous. It should not be dismissed because of relative inaccessability. Moreover, much of it is written in either German or English, a fact that should encourage us to persevere in obtaining copies. The second revealing aspect of these parts of the book is the different approach of continental ecologists. Great stress is placed upon objective numerical indices of dominance, affinities between species, and community delimitation, all of which subjects are more or less completely relegated to phytosociology by English and American ecologists. The progress that has been made in this branch of animal ecology may surprise many of them. Conversely, there is no emphasis at all upon population dynamics, which gets less than ten lines of print, including literature citations. This leaves a gap in the presentation that the reviewer finds difficult to understand.

With "Production Biology," the American reader is likely to be on more familiar ground. Balogh avoids the existing morass of overlapping terms in an admirable manner by relegating them to the single table of synonymy originally devised by Macfadyen. He concentrates attention on what is really being measured: the amount of living material at one moment, and changes in this amount over time. These can, of course, be translated into terms of bound energy by appropriate methods. He agrees with many authors in emphasizing the energy flow, since energy passes through the community, but matter is recycled in ways that make measurements unreliable or impossible. He recognizes three "energy paths" through the biocoenosis: storage in the bodies of plants and animals; the energy expended in life-processes; and the energy still bound in excreta and dead bodies. In citing measurements of the relative values for these, Balogh makes one of his most important points. This is that the primary energy path for terrestrial communities is through the decomposers. Thus, for the lepidopteran

[1] Balogh, János. 1958. Lebensgemeinschaften der Landtiere. Ihre Erforschung unter besonderer Berücksichtigung der zoozönologischen Arbeitsmethoden. Verlag der ungarischen Akademie der Wissenschaften, Budapest; Akademie Verlag, Berlin. 560 pp., 125 figs., 84 tables. $9.75.

Hyphantrea cunea, 16.6% of the energy taken in as food is "stored" in the body, 12.5% is spent in maintenance, and 70.9% leaves as feces. Without consulting Gere's original work, one cannot state the possible importance of overfeeding in these observations; but by way of corroboration, we do have Laurence's estimate that the biomass of insects in cow dung amounts to one fifth of the weight of the cow in a year. Balogh points out that the simple trophic level scheme must be modified to take account of this major energy path, and proposes a new series of levels among the animals that feed respectively on bacteria, detritus, feces, and dead animals. It scarcely seems worthwhile separating the last three; and the fungivorous species, including many mites and collembolans, should be added to the bacteria feeders. His main point is correct and well taken, however.

Some space is devoted to methods of measuring energy flow, and difficulties with various methods are discussed. It is concluded that bomb calorimetry is the method of choice whenever its use is possible.

The principal criticisms of the book are the above-noted lack of any treatment of population studies, and a failure to coordinate the 27-page bibliography with the text in an acceptable manner. It is disconcerting to find "Gere, 1956" cited in the text, and to discover five titles to which the citation could apply. Conversely, of three papers by Maucha cited in the text, two are not listed in the bibliography. The examples could be multiplied. The criticisms are minor compared to the usefulness of the book, which is printed on good paper, an excellent feature, considering the thumbing to which it is likely to be subjected.

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Aspects of Spanish Vegetation

The last two volumes of the Rübel Institute "Veröffentlichungen" contain an account of the International Phytogeographical Excursion in Spain (1953), 30 years after the first I.P.E. in the Swiss Alps (reported in Vol. 1 of the same series).

Part I[1] has 17 contributions by 16 authors. Ten are in German, 4 in French, 1 in Spanish, 1 in English, and 1 in Italian.

S. Rivas-Goday and E. F. Galiano, who with O. de Bolós were the principal hosts, lead with a general outline (in Spanish) of the itinerary (including a map). The trip lasted from June 25 to July 23 and involved some 40 participants, not all of them following the whole proceedings, however. This chapter gives a very brief account of the places visited and of their features of phytogeographical interest. As becomes quite clear upon the perusal of the rest of the volume, the group had well-focused common interests in historical plant geography and phytosociology.

S. Rivas-Goday's contribution (in German) is an outline of the vegetation of the Iberian Peninsula, illustrated with a new map in colour. He recognizes four formation-classes (sensu Rübel and Brockmann-Jerosch): *Durilignosa* ("Evergreen hardwoods"), *Aestidurilignosa* ("Mixed evergreen-deciduous hardwoods"), *Aestilignosa* ("Summergreen forest"), *Aciculilignosa* ("Needle-leaved evergreen forest") and *Frigorideserta* ("Alpine scrub and meadows"). These five major areas are subdivided into vegetation belts (*Vegetationsgürtel*) corresponding to climax areas (*Klimaxgebieten*). Each one of these is further subdivided into the classic Zürich-Montpellier classes, orders, alliances and associations. This general survey, however, does not venture to describe or define units below the class or the order. The author's extensive and intensive knowledge of the Spanish landscape in most of its parts allowed him to draw this very timely synthesis. His classification gives the student of Iberian vegetation his bearings, and the map is a most useful one.

E. Schmid attempts a review (in German) of even more ambitious geographical scope since he encompasses the mountainous areas, not only of the Iberian Peninsula but also of the Berber country and the Canaries. This appears as a further elaboration of his 1949 classification of vegetation zones of the Mediterranean area as a whole. In the latter, he had drawn attention to the *Laurocerasus Belt* and to other relict types within the orbit of the Mediterranean regimen, and in the present contribution he provides an extremely useful tabulation in graphic form (pp. 128, 158) of the geographic location of endemics and of their altitudinal position.

W. L. Kubiena's chapter on soils (in German), with its map of Spain, offers an important mise-au-point of del Villar's earlier work.

O. de Bolós' contribution (in French) concerns central Catalonia, and lists the major plant communities which are defined rather than described in terms of their "characteristics" and major places of occurrence (geographical, topographical or ecological, sometimes all three). H. Gaussen, on the contrary, provides a very descriptive account of the Spanish Pyrenees (in French) and offers a number of ombrothermic graphs for typical stations, as well as detailed distribution maps for *Fagus silvatica, Abies pectinata, Pinus silvestris* and *Pinus uncinata* in the Pyrenees as a whole. He also presents a very important map of the "geographic and ecological units" of the Pyrenees. Since this is the result of the work of many decades and since practically all the "units" have been visited by Gaussen and his collaborators, it allows him the best possible application of his concepts of the climate-soil-vegetation complex. The extremely varied topography and climate of the Pyrenees lends itself to the full play of many interpenetrations of presumed climax types and many inclusions of relict stands. Gaussen's *étage* is very similar to Rivas-Goday's *grado*. In fact, it is interesting to detect the influence of Gaussen's ideas and methodology in Spain and Portugal, where an earlier acceptance of the Montpellier approach has shifted a great deal in recent years.

Most of the other contributions are focused upon a special problem or a small group of plant communities. Thus, F. Sappa discusses (in Italian, with an English summary) the position of the semideciduous *Quercetum lusitanicae* in Spanish forest vegetation. F. Dupont considers the populations of limestone areas on the Vasco-esturian littoral (in French), where extremely poor and dry edaphic conditions exist under conditions of very high

[1] Lüdi, Werner (editor). 1956. Die Pflanzenwelt Spaniens. Ergebnisse der 10. Internationalen Pflanzengeographischen Exkursion (IPE) durch Spanien 1953. I. Teil. (Symposium). Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich, Heft **31**: 1-298, Figs. Verlag Hans Huber, Bern. DM/sFr. 29.40, $7.00.

atmospheric moisture. Lüdi's contribution (in German, with English summary) is purely floristic and complements Schmid's (with which it is not really tied up to any extent, however) by concentrating on the degree and kind of endemism at the alpine level. Lüdi, who edited the volume, also made an annotated compilation of the new stations and discoveries of vascular plants during the I.P.E. V. Allgorge and P. W. Richards (in English) and A. Lawallrée (in French) have done the same for the Bryophytes and the Ferns. Ingeborg Markgraf-Dannenberg has written on the genus *Festuca*.

M. Welten adds a much-needed study on pollen-analysis (in German). To this day, very little investigation by this method has been made in Spain and Portugal, and the addition of five new pollen diagrams to the earlier findings of Bellot and of Medina is indeed very welcome. Some remarkable features are: predominance of Ericaceous pollen in two profiles (Atlantic regimen) and its near-absence in the other three (Mediterranean regimen); the importance of *Corylus* and *Juniperus* in the north and their extreme reduction in the south; the much greater variety and abundance of arboreal pollen in the north and of grasses, sedges, and composites in the south.

H. Gams' contribution (in German) presents an account of the Tragacantha-Idelheiden ("thorny Tragacantha heaths") of the region that extends from the Caspian through the Black Sea to the Mediterranean. Through this now sharply differentiated area many taxa (e.g., of Euphorbiaceae, Ericaceae, Rosaceae, Leguminosae) have migrated. The present distribution of "heaths" from West to East: "Sukkulenten-Heiden," "Genisteen-Heiden," "Genisteen—Ericaceen Heiden," "Ericaceen-Heiden," "Tragacantha-Igelheiden" are in part the result of these historical movements. This is a valuable contribution to our understanding of the origins of the Mediterranean taxa and of the whole of the Mediterranean vegetation, and of its relation to the steppes of Eastern Europe and Central Asia where the center of origin of a number of important Leguminosae and Compositae probably lies. Another line of development attains the northwestern coast of Africa (and the Canaries?)—the "Sukkulenten-Heiden," and yet another the Ethiopian Highlands "Rosettenstrauch-Heiden."

A brief contribution (in German) by C. Regel compares Iraq and Spain. It touches upon some of the same problems, and points to a number of vicariant communities but without documenting them to the same extent.

The second part* (in German) has a definitely narrower scope, as it deals only with the "Euro-Siberian Phanerogamic plant communities of Spain." This means that it is limited essentially to the broadleaved deciduous forest climax-areas (of which four are recognized) and ventures very little into the domain of evergreen hardwoods. The Montpellier scheme of cataloguing vegetation is followed: sub-associations are grouped into associations, the latter into alliances; these into orders; thence into classes. Thirty of these latter, major units are presented here. They are broken down into more than 40 orders and these into about 75 alliances and a very large number of associations. The latter are named (with authorities), and very many are recorded in tabular form.

This approach is admittedly not very descriptive, and more indicative of phytogeographic affinities than of immediate conditions of the site. Fortunately a few sketches and some good photographs scattered throughout allow a more material perspective now and then.

The great value of this contribution stems from Tüxen and Oberdorfer's considerable knowledge of Euro-Siberian plant communities and their capacity to recognize in the Iberian Peninsula a number of associations that are near their boundaries. Although the cohesion of the associations does not break down, they present regional or local characteristics. It is no doubt for this reason that the authors see fit to propose new names for a number of variants, sometimes on the faith of one or two relevés! It would seem to me that an application of Lucy Braun's "association-segregate" theory to this vegetation would prove very useful.

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These two fascicles are hardly meant as a guide to the vegetation of Spain. Those not inured to the Braun-Blanquet system of nomenclature and reference will find the second one very hard to read. But it does contain a most richly documented compendium of Euro-siberian influences in the Iberian Peninsula. On the other hand, the more eclectic materials in the first fascicle provide a broader summary of the problems of West Mediterranean vegetation.

Those of us who are inclined to a "biosystematic" approach to the problems of taxonomy will miss a contribution along these lines. Such genera as *Adenocarpus, Cistus, Quercus, Phillyrea,* and others lend themselves at least to passing reference. This criticism would seem to be especially pertinent when addressed to a group that lays almost exclusive stress on the floristic composition of the plant community.

To all students of vegetation, the IPE reports are an inestimable source not only of information but also of education. Some of the more naïve claims for an "objective" approach to the study of vegetation can be dispelled by the kind of confrontation that the IPE has been carrying on for the past thirty-five years or so. Intimate association, in the field, *in the presence* of vegetation, on the part of scientists of different cultural and linguistic backgrounds as well as of different scientific trend or allegiance produces a many-sided picture and forces the emergence of unsuspected problems.

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* Tüxen, Reinhold, with Erich Oberdorfer. 1958. Die Pflanzenwelt Spaniens. Ergebnisse der 10. Internationalen Pflanzengeographischen Exkursion (IPE) durch Spanien 1953. II. Teil. Eurosibirische Phanerogamen-Gesellschaften Spaniens, mit Ausblicken auf die Alpine- und Mediterran-Region dieses Landes. Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich. Heft 32: 1-328, 27 Figs., 15 maps, 92 tables. Verlag Hans Huber, Bern. DM & sFr. 38.30, $10.75.

Mediterranean Plant Communities in the French Sector

Some 30 years of work are summarized in a recent book by Braun-Blanquet and his collaborators.[1] They have listed 23 classes, 35 orders, 57 alliances and more than 50 associations, with the conventional Latin names. Although the rationale for the recognition of associations and for grouping them into higher units has been expounded in the several editions of Braun-Blanquet's treatise and in some other works as well, we still lack a concrete exposé of how the Montpellier botanists proceed in the field and in the laboratory, how they solve the practical problem of applying the concepts of fidelity and constancy, and how they later assemble associations into alliances and devise even higher echelons in the hierarchy.

As an adept of the field method, I readily appreciate the guiding criteria in the choice of quadrat samples, in the application of scales of coverage and sociability, but I remain somewhat uncertain when it comes to the establishment of the higher units. In all fairness, it must be said that the opening statements on pages 7-13 are quite clear and that the theoretical basis for the choice of "characteristics" and "differentials" is well defined. What we do lack, however, is a model demonstration.

This is not provided by Guinochet (1955, Logique et dynamique du peuplement végétale), nor is it fully accounted for by Poore (1955, 1956, J. Ecol. **43**: 226, 245, 606, **44**: 28) or by Becking (1957, Bot. Rev. **23**: 411). In fact, to make it somewhat understandable to North American students it would have to be made in our own territory by allusion to our own flora. This has been done by Conard on Long Island (1935, Amer. Midl. Nat. **16**: 433) and in Iowa (1953, St. Univ. Iowa Stud. Nat. Hist. **19**, no. 4). Despite this admirable pioneering effort, it can be said that the Montpellier system of classifying vegetation remains almost untested in North America, and it is no exaggeration to affirm that it remains very widely misunderstood. It should be realized in the first place that the basic prerequisite of its application is a thorough familiarity with the flora of a large region (of the dimensions of, say, the Middle-West, the Southeast, New England, etc.), i.e., a region large enough to reach the confines of a climatic zone. The phytosociologist, *sensu* Montpellier, is able to name most of the plants on sight, has worked and collected extensively in the region and is acquainted with all the variants of vegetation within it, although he may have concentrated on certain types. (Should I point out that such habits are not being formed by too many students on North American campuses, and that this kind of competence is not common among their professors?)

In order to assemble the contents of a book such as this one, a vast experience is needed, a profound knowledge of historical plant geography and access to a great store of relevés made independently in the field. To be sure, a completely "objective" approach would consist in the manipulation of large numbers of such relevés in such a way that the "characteristic" species would automatically fall into place: fidelity ratings would result from a complete sampling of all the plant communities of an area, for instance. This has not been done anywhere, to my knowledge; and if it were possible, it is doubtful whether the necessary working enthusiasm could be generated to carry out the undertaking. What we have here is a grouping of plant communities in an order which largely reflects the *whole experience* of a small group of workers who are very close in their outlook, methods and means. They so often analogize the community and the species that it is tempting to say that if a "good species" is what a good taxonomist thinks it is, likewise a good association is as a good phytosociologist defines it.

There is a certain amount of agreement on this score in Europe; and although other means of tackling the problems of vegetation are sought and applied in Montpellier itself, there is wide recognition of the reality or at least of the usefulness of plant associations on the scale and by the criteria of the Montpellier School.

It can hardly be said that this form of listing plant communities is lacking in precision or in significance. A brief consideration of a sample association will show what kind of information is being made available and what implications can be read.

On pages 132-134 is described the association "Molinietum mediterraneum Br.-Bl. 1931." The name implies that it has been described by Braun-Blanquet in 1931 (full reference in bibliography of this volume) by the usual means of a chart (an example of which appears in the preface of the present book). An abstract of this chart is now given in the following form: 57 species are listed and they are grouped into blocks and for each a constancy and mean coverage coefficient are given. The first block lists the characteristics of the *association* and of the two recognized *sub-associations* (respectively *Serratula tinctoria* with coefficients of V and 1, and *Potentilla erecta* with V and +). The second block lists the characteristics of the higher order, the alliance (Molinio-Holoschoenion). The third block lists the characteristics of even higher echelons: the order (Holoschoenetalia) and the class (Molinio-Juncetea). The fourth block contains companion species of high presence, and the last block similar companions that predominate in one and not the other sub-association. There follows a statement on the number of relevés known and on the bibliographic sources for each of the sub-associations. A short paragraph also outlines the conditions of the site on which each unit is found. Thus, the Molinietum mediterraneum serratuletosum is "localized on the marshy edge of ponds of the Languedoc Plain on a substratum of recent alluvia. The ground-water level is high all year round (3 to 25 cm. deep). The soil is calcareous with traces of chlorides (0.02-0.1%) and a pH close to 7.5. This vegetation is disappearing and seems to have survived from glacial times."

If it is objected that the small number of samples provide little statistical security for the definition of associations, it can hardly be denied that a fine-textured book like the present one with its abstracts of innumerable field data provides a very solid network of reliable vantage points to all students of vegetation for a long time to come. One can only hope that many more intelligent inventories of this kind will be published in the years to come.

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[1] Braun-Blanquet, J., N. Roussine et R. Nègre. 1952. Les groupements végétaux de la France Méditerranéenne. 297 pp., 16 plates, & 3 tables. Centre National de la Recherche Scientifique (Service de la Carte des Groupements Végétaux) et Direction de la Carte des Groupements Végétaux de l'Afrique du Nord, Paris.

A Comparison of Two Different Schemes for Mapping Vegetation[1]

In the varied work in mapping vegetation in western Europe, two major systems are being applied. Under one E. Schmid of the University of Zürich has mapped the vegetation zones (*Gürtel*) of Switzerland on 4 sheets at the small scale of 1/200,000. Under the other Tüxen at Stolzenau in Germany has been mapping plant associations, as recognized by the Zürich-Montpellier school of phytosociology, at large scales of 1/10,000 to 1/25,000; and the French at Montpellier under Emberger, with Braun-Blanquet's aid and with G. Long as technical director, have launched a similar scheme.

The Plant Geography Commission of the Swiss Natural Science Association under the presidency of W. Lüdi has sponsored a test of the two methods. The reviewed monograph is the result. Of the two mappers, Moor has published a notable series of monographs on Jura vegetation using Braun-Blanquet's methods; Schwarz is a student of Schmid's, and a recent monograph of his was reviewed in this journal (vol. **38**(3): 546-7, 1957). The publication under review contains short essays by each cartographer describing his method of classifying vegetation, the ecology of the region mapped, and the vegetation found. The authors worked independently of each other. The resulting maps are at the scale of 1/10,000, 6.3 inches/mile, or 1 inch/277 yards. Considerable detail is thus possible, and Moor in fact maps the only occurrence within the area of an Arunco-Aceretum community occupying some 40 by 110 m. in a cool, wet, shaded couloir on a north slope. The original mapping was done to a scale of 1/5000.

The vegetation is predominantly beech forests of various kinds, with admixtures of other broad-leaved trees, some spruce, outliers of arctic-alpine plants, many open meadows both natural and used for hay and pasture, outliers of xeric Mediterranean and even continental vegetation, and specialized vegetation of rock faces and talus and scree slopes. Elevations range from 625 to 1466 m. Precipitation amounts to 1200 to 1600 mm/yr, evenly distributed, with ample winter snow. The high ridges are wind-exposed; rocky cliffs offer warm sites when they face south or cool, avalanche-swept sites when they face north.

Does one picture of the vegetation result from the two maps made by two different men laboring under two quite different ideas of what vegetation is and how it should be characterized? It does not. Schwarz' methods are ideally adapted to small-scale maps where one wants a landscape portrayal of the vegetation. Schmid's basic unit, the vegetation *Gürtel*, is in fact a rather gross unit for a 1/10,000 scale. Moor maps a smaller unit, associations and in some cases subassociations. These are ordered into higher units. Finally, Moor is mapping vegetation units; Schwarz is mapping the floristic aspects of landscape zones.

Agreement is evident on the plant species occurring; interpretations of these occurrences differ. The only real test of the variance in interpretations would be observations made on foot, in the region, in company with someone who knew the flora as well as Moor and Schwarz do. Certainly no abstraction from the field associations of plant species will satisfy everyone, and this perhaps as well as anything emphasizes the very human attributes of the mental molds which we use to cast our concepts of kinds of vegetation.

The essays by Moor and Schwarz which accompany the maps are good expositions of the respective methodologies of Braun-Blanquet and E. Schmid. It is hoped that those engaged in vegetation mapping will be stimulated by the essays to thorough study of the different viewpoints.

At first glance the altitudinal belts of different kinds of beech vegetation determined by climatic changes with altitude are better differentiated on Moor's map. On the other hand open and anthropogenic vegetation stands out more sharply on Schwarz's map. Closer study of the legends and the descriptions of the vegetation involved has convinced the reviewer at least that both maps portray the same vegetation, and that he can get a satisfying ecological understanding of the regional vegetation from either map. Since the Swiss maps are based on two such very different systems of vegetation classification, any agreement between the maps may be an argument for the reality of the vegetation units.

It is interesting to compare these maps with range survey type maps as made in the western U. S. Range type maps are less detailed since on smaller scales, but the most important difference is the use in range typing of simple physiognomic classification of vegetation. Unfortunately, although under such a physiognomic classification everyone agrees on many vegetation boundaries, the classification is incapable of refinement except by adding in the names of more and more dominant species. There are only a few vernacular names for physiognomically defined vegetation types, and an elaborate physiognomic system runs the danger of such a comment as Gaussen's on the "Macrophanerophytium": "I prefer forest." Unfortunately dominance types often cover up greater differences between vegetation types than they separate. The range survey types themselves suffer from another common weakness: All were set up by mutual agreement between range men having wide experience with western range vegetation. As a beginning this was fine. However no subsequent monographic study has ever been made of any range type. Thus, types like those characterized by *Coleogyne ramosissima, Cercocarpus ledifolius,* and *Purshia tridentata* have no place in the classification, and vegetations as spectacularly diverse as those characterized by *Wyethia amplexicaulis, Veratrum californicum,* and *Sieversia turbinata* (= *Geum rossii*), or *Artemisia nova* and *A. cana,* or *Bouteloua gracilis* and *Stipa lettermanii,* or *Populus tremuloides* and *Alnus rubra,* or *Sequoia sempervirens,* or *Picea engelmanii* and *Abies lasiocarpa* must be thrown together at present. As Moor emphasizes, a purely plant-sociological map forms the best basis for technological maps such as of forest or range types. A conclusion to be drawn from Moor and Schwarz' monograph is that study of vegetation must precede its mapping.

The monograph by Moor and Schwarz can be used as a model not only for the artistic printing of vegetation maps but also for the essential ideas which must underly any program of vegetation mapping. Agreement on vegetation concepts will be furthered by study of their work.

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[1] Moor, Max & Urs Schwarz. 1957. Die kartographische Darstellung der Vegetation des Creux du Van-Gebietes (Jura des Kantons Neuenburg). Pflanzengeographische Kommission der Schweizerischen Naturforschenden Gesellschaft, Beiträge zur geobotanischen Landesaufnahme der Schweiz, Heft **37**. 114 pp., figs., maps. Verlag Hans Huber, Bern. DM/sFr. 14.15, $3.40.

Forest Fires and Their Ecological Effects[1]

A burning forest is a distressing sight, but newly burned areas are still more depressing in their emptiness and lack of life. It is not rare that a whole forest burns down in a few days because of the reckless thoughtlessness of a smoking traveler, as is so often advertised near the roads in North America; but forest fires ignited by lightning or other natural forces are probably not rare. It has long been known that such fires have had a great influence on the ecology of the boreal regions, and they have doubtless been significant in determining the composition and even the extent of the forests themselves. Nowhere have trees grown undisturbed by fires for a very long period, and in the forests of the Canadian northlands very large areas show obvious signs of frequent fires in the past.

Forest fires are usually regarded as being devastating. It is less generally known that such fires under control have been found beneficial to a certain extent and that they have been used in that capacity in Sweden and elsewhere for at least a generation. It may seem peculiar that, although the ecological results of forest fires have long been recognized, only a few detailed studies on these effects have so far been undertaken. Very thorough studies, however, have lately been made on the invasion of vegetation into recently burnt areas in northern Sweden by Evald Uggla, who has reported on the results in two papers published in 1958. One of these publications is a rather short English summary of three recent studies, whereas the main results were printed in Swedish in the well-known Acta Phytogeographica Suecica, accompanied by many excellent pictures. It is a pity that this report is not in English so that it could be of more use to other than Scandinavian readers, for it is of the same high quality as other such papers from the ecological school of Uppsala. The extensive English summary is, however, very adequate and detailed.

Before going into details, the author describes the geography, topography, climate, geology, and forests in the area of the Muddus National Park which he has selected for this study. The Park is situated in northern Sweden just north of the Arctic Circle, in the region of conifer forests; but a large proportion of the area (45%) is covered with bogs, and about 15% of the forests are swamp forests. The climate is continental rather than oceanic. The dominant trees are *Pinus silvestris*, *Picea abies*, the two or three Scandinavian species of *Betula*, and *Populus tremula*.

Before describing his terminology and methods, the author gives a short historical review of forest fires in Sweden. It has been estimated that from 1876 to 1920 about 375,000 hectares of Swedish forests burned down, or 8300 hectares per year as an average, while during the ten year period 1944-1953 only 1673 hectares burned in the entire country.

The main study is concerned with the recovery of the vegetation in four areas which were burned in 1920, 1933, 1941, and 1947, respectively. Simple plots of 20 × 25 meters size were selected. Within these, twelve plots of 1/4 m^2 were established for analysis based on the Hult-Sernander-Du Rietz five-degree scale. More detailed studies were made in some plots, and belt transects were also used. The plots were analysed several times during a dozen years so that substantial information could be collected about the dispersal of the vegetation into the burnt areas.

The author summarizes his results by pointing out that a study immediately after a fire usually reveals that only the uppermost layer of the humus has been burned, and in humid depressions the vegetation may be undamaged. Also, runners and diaspores are found to survive at a few centimetres depth, despite the fact that the temperature at ground level may have reached 400-500°C. Many cooperating factors then decide in what way the primary succession will develop. Studies on the different species in vegetation layers are described in detail; and it is shown that although many species may have survived in protected pockets within the area of the fire, most species have invaded the area from the outside. Examples of the latter group are mainly wind-dispersed species like *Chamaenerion angustifolium*, *Populus tremula*, and *Betula*, whereas seeds of *Arctostaphylos* and *Calluna* seem to survive, as do also runners of *Vaccinium*.

The studies of the burned-over Swedish forests show that the ecological composition of the new forests may become very different after intense or moderate fires respectively, and the beneficial effect of the latter also varies considerably. But it is very apparent from this excellent study that moderate fires are of great importance in modern silviculture, especially when the subsequent seeding is controlled and based on the knowledge of modern plant breeding.

Forest fires are still considerably more common in North America than they are in Europe, for obvious reasons. On the other hand, ecological studies on their effects are rare on this side of the Atlantic. It is to be hoped, however, that long-time studies on forest fires and their effects will soon be commenced in different parts of this continent, since such programs will be invaluable to future silviculturists and also provide us with better explanations of the development of the vegetation cover in America in the past. Uggla's study will be of value for its account of European experience with forest fire, and for its bearing on the dynamics of boreal forests.

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[1] Uggla, Evald. 1958. Skogsbrandfält i Muddus Nationalpark. (Engl. summ: Forest fire areas in Muddus National Park, northern Sweden). Acta Phytogeographica Suecica **41**: 1-116, 61 figs., 8 plates, 16 tables. Almqvist & Wiksells Boktryckeri AB, Uppsala. Sw. kr. 21:—, $4.10.

Uggla, Evald. 1958. Ecological effects of fire on North Swedish forest. Almqvist & Wicksells Boktryckeri AB, Uppsala. 18 pp., 2 Figs.

The Algae[1]

Aside from conspicuous or spectacular phenomena, such as the sudden coloring, "blooming," or sliming of lakes and ponds, the occurrence of "red tides" in the sea, or the entanglement of fish hooks by pond scum, the layman seldom observes or hears of the algae. Hence it is unusual to see a sprightly book, "aimed at the general reader," which deals with this interesting and important group of plants in a manner that can be understood and appreciated by the intelligent layman or general student. It is to Tiffany's credit that he has succeeded as well as he has in presenting a complex subject clearly, in general language, within the confines of far too few pages. The almost complete lack of common names for algal species has made the author's task more difficult, and undoubtedly the number of his readers has been reduced by the unavoidable liberal sprinkling of generic names that are strange to the ears and eyes of the general reader.

Tiffany's book is profusedly illustrated by excellent drawings and photographs (it is unfortunate that the two color plates of the first edition have had to be replaced). None of the illustrations has any precise indication of magnification, and the uninformed layman may therefore obtain a garbled view of the relative sizes of diverse algae, such as diatoms and kelps. It is true that the uninitiated reader usually does not have at his command a system of measurement adequate for the description of microscopic dimensions; but perhaps it is no more difficult for him to learn about millimeters and microns than about Ångstrom units, and the latter are used by Tiffany in discussing the wave lengths of radiant energy.

In the 20 years since the appearance of the first edition (1938), there have been great advances in our knowledge of the algae, especially of culture methods, and of algal ecology and physiology. Tiffany has chosen to leave the original 13 chapters of the first edition with only minor modifications to bring them up to date. Most of the new material is included in a new chapter (chapter 12) entitled "Algae and research." In the 8 pages of this chapter the author gives greatest space to recent studies of the use of algae as food by man, and to the Florida "red tide," caused by the dinoflagellate, *Gymnodinium brevis* (thanks to newspaper publicity this is one of the few species of algae with a widely known common name—"Jim Brevis"). A good deal of space is devoted also to a discussion of the chemical events of photosynthesis. Other areas of advance either are described in brief paragraphs or are omitted entirely (e.g., the important studies of photosynthesis as a measure of primary production, of the occurrence of algal antibiotics and probiotics, etc.).

A book such as Tiffany's is not intended to give a complete picture of the subject under discussion, but rather to stimulate interest, which will lead to further, more intensive study. The appearance of a second edition suggests that this aim has been accomplished.

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[1] Tiffany, Lewis Hanford. 1958. Algae: the grass of many waters. 2nd edn. Charles C. Thomas, Springfield, Ill. xv + 199 pp. 13 figs., 41 plates. 4 tables. $6.50.

Animal Behavior[1]

A long career of research in animal behavior is the excellent background of the author, who is Chairman of the Division of Behavior Studies at the Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine.

Behavior and social organization certainly belong to the central problems of human existence. This fact may be one of the deeper reasons the living creature has fascinated the human spirit for a long time. Ethology, the comparative study of animal behavior, has recently developed into a modern branch of zoology; many of its results are of basic importance for understanding the principles and the organization of life. In his study, Dr. Scott has brought together the most important problems, results and objectives of this science, and contributed a good deal of his own first-hand observations and conclusions.

In comparing animal and human behavior, he introduces the reader to the world around us, states and explains a set of important terms, and discusses the general ideas and methods of study, without being too theoretical. Behavior occurs as a response to stimuli, which come from inside the organism, or from the physical and social environment. The next step leads to the discussion of the underlying physiological and anatomical mechanisms affecting behavior. The author gives a detailed survey on the complex network of internal mechanisms and causations. In the chapter on neurophysiological considerations, Dr. Scott could have reviewed the Reafference Principle which was suggested by v. Holst and Mittelstaedt; it can explain certain phenomena that the reflex theory interprets erroneously.

Special emphasis is given to the problems of the adaptation of behavior to the environment, including the general principles of learning, the importance of experience, intelligence, communication, and social organization.

In the chapter "Heredity and Behavior," the author explains why he avoids the unfortunate and often misused term "instinct," stating that "from the viewpoint of genetics there is no possible way in which behavior as such could be biologically inherited through the chromosomes." He suggests this term as a general, descriptive one applied to behavior *differences* which are largely determined by heredity.

In this connection, the reviewer is inclined to remind of the fact that ethology, for many years, has placed the exploration of hereditarily fixed behavior patterns in the foreground. As early as 1873, Spalding anticipated the modern concept of ethology, which emphasizes that there are many rigid behavior patterns which are completely hereditarily fixed. In 1955, to give one remarkable example, it was shown by S. v. Hoermann, who hybridized two closely related species of crickets, that in three features of behavior patterns the inheritance was monofactorial. The author agrees with these facts, stating that heredity sets the general patterns of behavior, or in other words, that most of the basic behavior patterns do not change; they are the "fixed patterns" in the terminology of European ethologists. Two other facts are pointed out

[1] Scott, John Paul. 1958. Animal behavior. University of Chicago Press, Chicago. viii + 281 pp., 33 figs. & 43 photographs. $5.00.

in this chapter. The first is the important result that basic patterns can be suppressed by certain stimuli. The second involves Mr. Scott's noteworthy Mendelian experiments with dogs, which were kept over several generations under constant conditions: In most cases more than one gene affected the inheritance of a particular behavior characteristic, and heredity modified either variability or habit formation and tipped the balance between them. This conclusion was often neglected by ethologists who discussed behavior problems, and it is worthwhile to note the mutual influence of heredity and environment as two complementary forces.

All in all, this is an instructive and well-illustrated account of animal behavior, including a rich collection of valuable details and general considerations. It may be noted with special gratification that the author mentions a good collection of behavior studies in lower animals, starting with the important work of Jennings. Finally, I wish to say that the text is written in such a clear style, avoiding difficult theoretical constructions, that the general reader, interested in living nature, can understand this useful introduction to animal behavior without outside help.

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Acoustic Orientation in Animal and Man[1]

With his studies of the orientation of bats and birds, D. R. Griffin, professor of zoology at Harvard, has become famous on every campus of zoologists around the world. His preferred animal is the bat, the only expert flier among mammals, and a highly exciting creature. For most of us it is no more than a whisking shadow casually seen in the evening twilight, yet how much more Griffin knows about these wing-handed mammals!

This interesting and outstanding monograph about the different methods of acoustical orientation in animals and in men is the result of serious studies and inquisitive approaches to some most obscure details. And yet, Griffin never has forgotten the view for the whole, and he describes implications of the widest kinds.

The main story is a careful introduction into the world of bats. Stemming from nocturnal insectivores, some sixty million years ago, bats themselves are active at night, generating their own sounds, blowing them through their open mouth or nostrils, and locating obstacles and prey through perception of the reflected sound waves by means of their own ears. A wide scale of methods of echolocation in bats is described, and only some of the vegetarians among them, flying foxes and most of their relatives, depend entirely on visual orientation.

Special laryngeal mechanisms proved to be responsible for these ultrasonic sounds which reach 50,000-100,000 c.p.s., and which are inaudible for human ears. Probing their environment, bats emit short impulses of these high-frequency sounds, each lasting for only one or some few milliseconds.

Further on, Griffin leads the reader into the scientist's workship, tells about the great difficulties and problems for the experimental approach and scientific argumentation. He demonstrates the success and failure of the acoustical orientation of bats during critical tests. Sonagrams illustrate the clicks and tones of the unique animals. Many unsolved facts are discussed; one of them is the astonishing long-distant homing of displaced bats. How could they do it by echolocation?

It is to Griffins credit that he graciously acknowledges the independent discovery (during World War II) of echolocation in European bats by the Dutch scientist Dijkgraaf and the German zoologist Möhres.

It is not only the bat which shows this highly specialized ability. Turning to other animals, Griffin clarifies the great importance of sound localization in the animal kingdom. Moths, for example, hearing the insectivorous bat pursuing them, either react with erratic flights, or they immediately drop to the ground, remaining motionless until the danger passes. Not only insects, also fish, amphibians, and mammals, including blind men, have developed particular methods of acoustical orientation. Very stimulating are the chapters on hearing and sound production in marine mammals, such as the whale and the porpoise. Here, Griffin opens a window to a wide unknown field for future research.

The book also fascinates the reader with the stories about two birds which have become famous together with their investigators. The first one is the peculiar Oilbird from Caripe in Venezuela. There it inhabits deep caverns, and it is capable of accurate flight in absolute darkness. It was Griffin who detected its orientation by echolocation. These birds produce similar short clicks, but lower pitched than those of bats. The second bird is a South East Asian Swiftlet, well known to the gourmets because of its edible nests, mainly built of salivary secretions. A. Novick, a collaborator of Griffin, brought the proof of echolocation for this bird.

Parallels between the orientation problem of blind men and bats, showing a common auditory basis for obstacle detection, and a chapter about artificial devices for human echolocation conclude this excellent publication. It is rich in interesting facts, profound ideas, and prognostic theses. It may be called a remarkable recent edition on modern advances in zoology. The material seems to deal with a highly specialized field; but it has proved to be of general importance, and thus, this book is written for all who are deeply interested in the wonderful living world around us.

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[1] Griffin, Donald R. 1958. Listening in the dark: the acoustic orientation of bats and men. Yale University Press, New Haven. xviii + 413 pp., 16 plates, 15 figs., 12 tables. $7.50.

Natural History of the Colonial Birds of Great Salt Lake[1]

More than two-thirds of this book deals with the natural history and population trends of four species of colonial-nesting birds on the islands of Great Salt Lake. The rest consists of descriptions of the physiography and vegetation of the islands, distribution notes on the Caspian tern, a list of birds known to occur on the various islands, historical accounts of three refuges on the lake, and an evidently thorough bibliography of about 250 items. The account of the Bear River Migratory Bird Refuge includes a check list of birds that is said to be applicable to the whole Great Salt Lake region.

The four species dealt with at length are California gull, white pelican, double-crested cormorant, and great blue heron. About 50 pages are devoted to each of the first two species and about 15 apiece to the second two. Such subjects as history of the colonies, migration, reproductive biology, and food habits are discussed for each species; and several additional topics (flight, voice, plumages and molts, etc.) are included for the gull and pelican.

The sections on history of the colonies present detailed listings of shifts in colony size and location. Apparently this information is difficult to interpret at present, but it is potentially valuable to future students of population dynamics. Results of banding are given in considerable detail, but little use is made of the data other than tracing post-breeding dispersal. In most cases, the data are not numerous, but calculations of mean annual mortality, mean after life time, and so on would have been interesting. On page 122, *average life expectation* in the white pelican seems to have been confused with *potential natural longevity* (see Farner, p. 399, in Wolfson, 1955, Recent studies in avian biology). On the basis of 72 returns and recoveries of pelicans banded as young (given on page 123), the average life expectation as of the date of banding appears to be less than one year, rather than more than eight as Behle suggests. The discussions of food habits are complete and interesting, particularly the section on the California gull. In some cases, scientific names of food items seem to have been copied uncritically from the original investigator. The resulting use of an occasional out-of-date name may prove annoying to some users of the book.

Ecologists interested in niche relations of birds will wish that the section "The choice of these islands as nesting sites" were longer. Behle suggests that the primary reason for utilization of the islands by the four species is inaccessibility to predators. Apparently this advantage outweighs, at least for these large birds, the disadvantages of having to travel 25 to 50 miles to food and of lacking nesting materials. A thorough ecological study of the problems of occupancy of the islands would be worthwhile. For example, what role, if any, does the difficulty of maintaining a favorable water balance in the face of such highly saline drinking water play in restricting other species from nesting on the islands?

On its own terms, as a compilation of what is presently known and a starting point for future research, the book is a success.

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[1] Behle, William H. 1958. The bird life of Great Salt Lake. University of Utah Press, Salt Lake City. xiii + 203 pp., 43 figs., 28 tables. $4.50.

The Bobcat of North America[1]

This monograph on the bobcat completes the author's discussion of the natural history and economic value of four large North American predators: the wolf, puma, coyote and bobcat.

Although Mr. Young modestly confesses that his four monographs are far from the last word on the species discussed, he was well qualified to write them since he worked for thirty-eight years on predator problems for the Biological Survey and the Fish and Wildlife Service.

The reviewer, who has read Mr. Young's previous books with interest, again enjoyed this volume, particularly the many interesting quotations of observations by woodsmen. It stands to reason, considering the author's past experience, that the chapters on economic status and hunting and control are best authenticated. Other chapters include a discussion of the distribution, habits and characteristics, parasites and diseases, and the races of the bobcat. The author's main contribution is that he brought considerable information on the life history and management of the species together in a readable book.

For reasons explained below, Mr. Young's most recent effort is less commendable than his previous ones:

1. The book is neither a popular account, nor a satisfactory biological treatise. The author made efforts to popularize his writing, as evidenced by such naturalistic jargon as found on page 28: "The animal may seek its prey either in daylight or night, for it posseses eyesight seemingly as sharp as that of a crow, and at night comparable to that of an owl."

2. Sections of the book seem poorly organized. This is particularly true for the chapter on parasites and diseases, in which ecto- and endo-parasites are mixed up in the discussion.

3. Some quotations are excessively lengthy. These could have been reduced and still illustrate the point the author was trying to stress. Parts of some quotations are irrelevant.

4. References to figures are sometimes inadequate.

5. Sometimes more reference to the authors of certain studies should have been made.

The number of typographical errors is not serious. One obvious misprint on page 17, Table I is "winter 1958." On page 48 there is a paragraph in small print under Table 8. It is not clear whether this is supposed to be a footnote of this table, or part of the text. The illustrations are generally good but could have been more carefully screened. Some line drawings are inadequate.

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[1] Young, Stanley P. 1958. The bobcat of North America. The Stackpole Company, Harrisburg, Pennsylvania; and the Wildlife Management Institute, Washington, D. C. 193 pp., illus. $7.50.

Daphnia[1]

The extreme variability of *Daphnia* makes its taxonomy difficult and interesting. Since evolutionary and ecological studies require a foundation of sound taxonomy, Brooks' magnificent monograph is of considerable importance.

The monograph is divided into several sections: there is a discussion on techniques, a key based on mature females, descriptions of species found in North America including diagnoses, ecology, large illustrations and distribution maps, and a division of the North American continent into ten areas, describing the species in each, and giving their habitats.

Brooks believes that he has found populations which combine the characters of two species and that there is evidence for introgression. Daphnia species in temporary ponds are usually large in size. A tremendous amount of interesting information is distributed through the text of the monograph.

I have only two criticisms. One concerns the distribution maps; the shaded area indicates the conjectured range for each species, which often extends far beyond the known range as indicated by dots, and for which there is usually no evidence. The other is that the high price of the monograph will probably limit the circulation of this useful paper.

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[1] Brooks, J. L. 1957. The systematics of North American Daphnia. Memoirs of the Connecticut Academy of Arts & Sciences, vol. 13, p. 1-180, 61 plates. $8.00. Also, Yale University Press, New Haven.

Evolution as a Process[1]

This is not intended to be just a collection of essays on the subject of evolution, as is so often the case, in which each author merely studies in detail a limited process. Instead it was the principal editor's aim to show that evolution could be studied as a unitary process, that all evolution is underlain by a single genetic mechanism, namely, that of *environmental selection acting upon genetic diversity*. With this intent, essays were written by nineteen persons and collected into this volume.

Julian Huxley himself has written the introductory essay. Here he describes the reasons why he feels that evolution is not just the study of separate processes. It is pointed out that evolution takes place in relation to the environment and that the same kinds of long-term trends are apparent in all groups, namely, specialization, advance in general efficiency, adaptive radiation and, usually, restriction and final stability. He might also have indicated, final inability to change followed by extinction when the environment changes. Interestingly enough the same long-term trends are apparent in the evolution of human knowledge. This has been pointed out by Huxley in the evolution of the study of evolution itself.

The sixteen individual essays in this book concern themselves with various aspects of the subject. R. A. Fisher in a "Retrospect of the Criticisms of the Theory of Natural Selection" points out that all criticisms have in principle been answered by mendelian genetics. Of interest to ecology, he states that selection is not usually a matter of life or death, but of slight differential survival. J. B. S. Haldane writes of the reasons why, though selective forces may be intense in their action on a population, they are usually in approximate equilibrium; thus variance is conserved in populations otherwise making for uniformity. E. Mayr discusses microevolutionary problems of great interest to the field ecologist and taxonomist. This stimulating and possibly significant paper is primarily speculative at this time; but it is to be hoped that speculation may later lead to experiments on the application of genetic principles to field populations.

E. B. Ford discusses many of the same problems in a general way, and P. M. Shepard in a more specific way. Shepard follows Ford's general contention—which is generally agreed upon—that selection is more important to evolution than random drift. H. B. Cott reviews the subject of allaesthetic characters, those whose evolution is controlled by the sensory perceptions of other species or individuals. H. N. Southern discusses this problem in relation to the color and pattern of cuckoo eggs. Apparently these eggs are differentiated geographically; Southern regards this condition as intermediate between true polymorphic forms and geographical races. Allaesthetic characters are also described by N. Tinbergen, but in this case the characters are courtship display. Close analysis of the display patterns indicates that the patterns were developed secondarily as by-products of other habits of the species, not directly for their own use.

E. N. Willmer strikes a possible blow at some phases of mimicry theory by suggesting that there is no evidence that any placental animal other than the primates has color vision. On the other hand, there is good evidence that birds, reptiles, and some fishes and amphibia have a color sense. Color vision has evolved independently, in all likelihood. D. Lack shows the relation of natural selection to clutch size in birds; the number of eggs laid by a species of bird is higher in higher latitudes. The basic clutch size is adaptive, adjusted by selection in relation to food supply. Sociality among birds is also adaptive, according to J. Fisher. The advantages of social behavior are apparent in territorial behavior, food habits, breeding behavior and social display.

B. Rensch considers the effect of increased body size on the relative size of the brain and its functions. He favors the view that the increase of body size leads to a relative size increase of the higher sensory regions of the cerebral cortex. A. C. Hardy argues that Haeckel's "Law of Recapitulation" is false and that many of the sequences read into that law should be read in reverse. He suggests that many lines of evolution are paedogenetic—the prolongation into sexually mature life of juvenile characters. G. R. de Beer supports this contention in reviewing Hadzi's views on animal evolution, suggesting, for example, that the ctenophores are derived from flatworms by paedogenesis, rather than being (possibly) near their ancestry. These papers may suggest some reconsideration of the significance of paedogensis in evolution, of the extent to which "primitive" organisms and characters may be secondarily so.

[1] Huxley, Julian, A. C. Hardy & E. B. Ford (editors). 1954. Evolution as a process. (Symposium). 367 pp. Allen and Unwin, London; Macmillan, New York. 25/, $4.25.

S. Westoll shows that the relation between mountain building and evolution is not all one of major crises followed by extinctions, but also a series of minor earth movements followed by altered ranges of ecological conditions, new adaptive circumstances and migrations. E. T. H. Corner describes the evolution of the tropical forest, with the indication that the evolution of ecological communities demands attention to new ways of life and the interaction between their representatives. S. Zuckerman studies the correlation between morphological characters in the evolution of the higher primates. L. Z. Young considers the relation between heredity and memory, though different from that of evolutionary adaptation, to be concerned with adjusting the organism to changes in the environment.

All together, this is an excellent collection of essays. For the ecologist, interest will depend on the particular phase of ecology in which he is working, though I think that much will be found in these pages of interest to anyone. It does not, perhaps, really fulfill the editor's intent; for it is a wide range of particular evolutionary phenomena that are discussed, rather than evolution as a general, unitary process; but the book has in consequence a wide range of interest.

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Excerpta Botanica, Sectio B: Sociologica

Beginning in 1959, the Gustav Fischer Verlag in Stuttgart will publish a new international bibliographic journal, which is to cover the whole plant-sociological literature of the world. The journal will bear the title given above, and will appear in four numbers each year.

The publication will be carried out in cooperation with the International Society for Plant Geography and Ecology (Internationalen Vereinigung für Vegetationskunde, Association Internationale de Phytosociologie), with collaboration of numerous specialists in individual countries. The responsible editor will be: Prof. Dr. R. Tüxen (Zentralanstalt für Vegetationskartierung), Schinnaer Landstr. 6, Stolzenau/Weser, West-Germany (as Secretary of the International Society for Plant Geography and Ecology).

Sectio A: Taxonomica et Chorologica of the Excerpta Botanica will be edited in ten numbers per year by Drs. H. Melchior, W. Robyns, R. C. Rollins, G. Taylor, and E. Werdermann, and will carry abstracts from the area of Systematics and Chorology in a broader sense.

Arid Zone, a Newsletter

Arid zone research has become a major project of UNESCO, involving various programs and many scientists and administrators in the region from North Africa through the Middle East to South Asia, and in other parts of the world. To assure the best possible liaison among these activities and specialists, it has been found necessary to publish regular progress reports; such is the purpose of the new newsletter.

Entitled "Arid Zone: Newsletter about Unesco's Major Project on Scientific Research on Arid Lands," it is to be published regularly for the benefit of Member States, their National Commissions, their cooperating committees for the Major Project, appropriate international scientific organizations, and all scientists collaborating with UNESCO in this field. There were two issues in 1958, in English and French. Beginning in 1959, it is planned to publish the Newsletter quarterly in an expanded form. News about projects or achievements of interest to everyone concerned with arid zone problems will be included. However, the Newsletter will not publish technical articles better suited to specialized journals.

The Secretariat would be grateful for assistance in securing the widest possible circulation for this Newsletter. Readers are asked to indicate how many copies they wish to receive regularly in English or French, and to communicate the addresses of institutions or persons who they believe would be glad to receive this publication in either language.

The first numbers have been received by the review editor from UNESCO (19 avenue Kléber, Paris—16e, France). Recent issues of another publication, the symposium series Arid Zone Research, will be found under UNESCO in the list following.

BOOKS AND MONOGRAPHS RECEIVED FOR REVIEW

Anderson, A. W. & E. A. Power. 1957. Fishery statistics of the United States—1955. U. S. Dept. Interior, Fish & Wildlife Service, Washington, Statistical Digest **41**: 1-446, num. tables, figs. $2.00.

Balduf, W. V. 1959. Obligatory and facultative insects in rose hips; their recognition and bionomics. Illinois Biol. Monog. No. **26**: 1-194, 12 plates, 3 tables. Univ. Illinois Press, Urbana.

***Barkman, J. J.** 1958. Phytosociology and ecology of cryptogamic epiphytes, including a taxonomic survey and description of their vegetation units in Europe. van Gorcum & Comp. N. V., Assen. xiii + 628 pp., 20 figs., 50 maps, 16 plates, & 71 association tables. Hfl. 44.00, $12.00.

Beklemischev, W. N. & N. K. Shipitsina. 1957. Seasonal phenomena in the life of anophelene mosquitoes of the U.S.S.R. (In Russian). Travaux de l'Institute de Parasitologie Médicale du Ministère de la Santé Publique de l'U.R.S.S., Moscow. 527 pp., tables & figs.

Bodenheimer, F. S. 1958. The history of biology: an introduction. Wm. Dawson & Sons Ltd., London. 465 pp., 37 figs., plates. 42/, $6.00.

Bonner, John Tyler. 1959. The cellular slime molds. Princeton Univ. Press, Princeton. viii + 150 pp., 13 figs. $4.00.

Brown, Clair A. 1959. Vegetation of the Outer Banks of North Carolina. Louisiana State Univ. Studies, Coastal Series No. **4**. x + 179 pp., 50 figs. Louisiana State Univ. Press, Baton Rouge. $3.00.

***Brown, Vinson.** 1954. The Sierra Nevadan wildlife region—its common wild animals and plants. Naturegraph Co. (American Wildlife Region Series, Vol. 2), San Martin, Calif. 80 pp., 1 map, 350 figs. $1.00 paper, $1.75 cloth bound.

***Brown, Vinson.** 1957. The California wildlife region—its common animals and plants. Rev. ed. Naturegraph Co. (American Wildlife Region Series, Vol. 1), San Martin, Calif. 128 pp., 1 map, 3 photos, 550 figs. $2.50 paper, $3.75 cloth bound.

***Brown, Vinson, Charles Yocom, & Aldene Starbuck.** 1958. Wildlife of the Intermountain West. Naturegraph Co. (American Wildlife Region Series, Vol. 4), San Martin, Calif. 144 pp., 14 photos, 2 maps, 550 + figs. $2.50 paper, $3.75 cloth bound.

Carthy, J. D. 1958. An introduction to the behaviour of invertebrates. Macmillan Co., New York. xiii + 380 pp., 148 figs., 15 tables. $8.00.

Dasmann, Raymond F. 1959. Environmental conservation. John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. x + 307 pp., 153 figs., 12 tables. $6.50.

Daubenmire, R. F. 1959. Plants and environment: a textbook of plant autecology. 2nd ed. John Wiley & Sons., Inc., New York; Chapman & Hall, Ltd., London. xi + 422 pp., 29 figs., 14 tables. $6.95.

Dubos, Rene. 1959. Mirage of health; utopias, progress, and biological change. Harper & Bros. (World Perspectives, Vol. 22), New York. xviii + 236 pp. $4.00.

Edds, Mac V., Jr. (editor). 1958. Immunology and development. (Developmental Biology Conference Series, 1956). Univ. Chicago Press, Chicago; Cambridge Univ. Press, London; & Univ. Toronto Press, Toronto. xi + 58 pp., 2 tables. $2.50.

Essig, E. O. 1958. Insects and mites of western North America. 2nd ed. Macmillan Co., New York & London. xiii + 1050 pp., 766 figs., taxonomic keys. $18.00.

Ferry, James F. & Henry S. Ward. 1959. Fundamentals of plant physiology. Macmillan Co., New York & London. ix + 288 pp., 130 figs., 44 tables. $6.50.

Foster, Adriance S. & Ernest M. Gifford, Jr. 1959. Comparative morphology of vascular plants. W. H. Freeman & Co., San Francisco. xi + 555 pp., 213 figs. $9.00.

Francis, Carl C. 1959. Introduction to human anatomy. 3rd ed. C. V. Mosby Co., St. Louis. 548 pp., 324 figs., 29 color plates. $5.75.

Gabrielson, Ira N. & Frederick C. Lincoln. 1959. The birds of Alaska. Stackpole Co., Harrisburg, Pa., & Wildlife Management Institute, Washington. xiii + 922 pp., 12 color plates. $15.00.

Galoux, A. 1951. Les principales essences forestières de l'Amérique Septentrionale tempérée; leur introduction en Belgique. Station de Recherces de Groenendaal, Travaux, Sér. B, No. **13**: 1-141 pp., 23 figs., tables. Groenendaal (Hoeilaart), Belgium.

Galoux, A. 1951. Les forêts de l'Amérique Septentrionale tempérée (études écologiques). Station de Recherches de Groenendaal, Travaux, Sér. A, No. **7**: 1-95, 46 figs. Groenendaal (Hoeilaart), Belgium.

Gislén, Torsten & Hans Kauri. 1959. Zoogeography of the Swedish amphibians and reptiles, with notes on their growth and ecology. Acta Vertebratica, Vol. **1**, No. 3: 197-397, 69 figs., 26 tables. 40:— Sw. kr., $7.75. Almqvist & Wiksell, Stockholm.

Grant, Verne. 1959. Natural history of the phlox family. Vol. 1. Systematic botany. Martinus Nijhoff (International Scholars Forum, Sciences, Vol. 1), The Hague. xv + 280 pp., 79 figs., 14 tables. 19.—guilders, $5.00.

***Hauser, Philip M. & Otis Dudley Duncan** (editors). 1959. The study of population; an inventory and appraisal. (Symposium) Univ. Chicago Press, Chicago; Cambridge Univ. Press, London; & Univ. Toronto Press, Toronto. xvi + 864 pp., 15 figs., 75 tables. $15.00.

Hicks, Ellis A. [1959]. Check-list and bibliography on the occurrence of insects in birds' nests. Iowa State College Press, Ames. 681 pp. $8.50.

Hitchcock, C. Leo, Arthur Cronquist, & Marion Ownbey. 1959. Vascular plants of the Pacific Northwest. Part 4: Ericaceae through Campanulaceae. Univ. Washington Press, Seattle. 510 pp., num. figs., taxonomic keys. $12.00.

Hoff, C. Clayton. 1959. The ecology and distribution of the pseudoscorpions of north-central New Mexico. Univ. New Mexico Publ. No. **8**: 1-68 pp., 5 figs., table, taxonomic key. $1.50. Univ. New Mexico Press, Albuquerque.

***Hubbs, Carl L.** (editor). 1958. Zoogeography. (Symposium). American Association for the Advancement of Science, Washington, Publ. No. **51**, x + 509 pp., 115 figs., 13 tables. $12.00.

***Keay, R. W. J.** 1959. Vegetation map of Africa south of the Tropic of Cancer. (English with French transl. by A. Aubréville). Oxford University Press, London & New York. 24 pp., colored map. $2.40.

Keen, A. Myra. 1958. Sea shells of tropical West America; marine molluscs from Lower California to Colombia. Stanford Univ. Press, Stanford, Calif. viii + 624 pp., num. figs. & 10 color plates. $12.50.

Knapp, Rüdiger. 1958. Einführung in die Pflanzensoziologie. I. Arbeitsmethoden der Pflanzensoziologie und Eigenschaften der Pflanzengesellschaften. 2nd ed. Verlag Eugen Ulmer, Stuttgart. 112 pp., 34 figs., 17 tables. DM 6.30, $1.50.

Lowenthal, David. 1958. George Perkins Marsh, versatile Vermonter. Columbia Univ. Press, New York. xii + 442 pp. $6.50.

Lüdi, Werner (editor). 1958. Verhandlungen der vierten internationalen Tagung der Quartärbotaniker in der Schweiz vom 6.-16. August 1957. (Symposium). Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich, Heft **34**: 1-175, figs. & tables. DM 16.50, $4.00. Verlag Hans Huber, Bern.

Lüdi, Werner (editor). 1959. Ergebnisse der internationalen pflanzengeographischen Exkursion durch die Ostalpen 1956. (Symposium). Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich, Heft **35**: 1-143 pp., figs. & tables. DM 15.00, $3.60. Verlag Hans Huber, Bern.

***McCormick, Jack.** 1959. The living forest. Harper & Bros., New York. viii + 127 pp., figs. $3.95.

Manning, T. H. & A. H. Macpherson. 1958. The mammals of Banks Island. Arctic Institute of North America, Tech. Paper No. **2**: 1-74, 35 tables, 15 figs. $2.00.

Marcuzzi, Giorgio. 1956. Fauna delle Dolomiti. (Fauna of the Dolomitic Alps). Istituto Veneto di Scienze, Lettere ed Arti, Classe de Scienze Matematiche e Naturali, Memorie, Vol. **31**: 1-593, 73 figs., 16 plates. Venice.

Martin, Paul S. 1958. A biogeography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico. Univ. Michigan, Museum of Zoology, Miscellaneous Publ. No. **101**: 1-102, 7 figs., 4 maps, 7 tables, 7 plates. $1.50. Ann Arbor.

Mills, Harlow B. et al. 1958. A century of biological research. Illinois Natural History Survey, Urbana, Bulletin, Vol. **27**, Art. 2: 85-234, figs.

***Misra, R. & G. S. Puri.** [1958]. Indian manual of plant ecology. The English Book Depot, Dehra Dun. x + 341 + xiv pp., 56 figs., 111 tables. Rs. 15.50, $3.10.

Mozley, Alan. 1959. Ecological processes. H. K. Lewis & Co. Ltd., London. xi + 68 pp. 9/, $1.30.

***Odum, Eugene P. & Howard T. Odum.** 1959. Fundamentals of ecology. 2nd ed. W. B. Saunders Co., Philadelphia & London. xvii + 546 pp., 160 figs., 32 tables. $7.50.

Olsson, Viking. 1958. Dispersal, migration, longevity and death causes of *Strix aluco, Buteo buteo, Ardea cinerea* and *Larus argentatus;* a study based on recoveries of birds ringed in Fenno-Scandia. Acta Vertebratica, Vol. **1**, No. 2: 89-189, 23 figs., 15 tables. Sw. kr. 20:—, $3.85. Almqvist & Wiksell, Stockholm.

Patterson, W. Bradford (editor). 1959. Wound healing and tissue repair. (Developmental Biology Conference Series, 1956). Univ. Chicago Press, Chicago; Cambridge Univ. Press, London; & Univ. Toronto Press, Toronto. xi + 83 pp., 25 figs., 5 tables. $2.75.

Power, E. A. 1958. Fishery statistics of the United States—1956. U. S. Dept. Interior, Fish & Wildlife Service, Washington, Statistical Digest **43**: 1-476 pp., num. tables & figs. $2.25.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Fisheries Research Board of Canada Bulletin No. **119**: 1-300, num. tables, figs. $5.00. Queen's Printer & Controller of Stationery, Ottawa.

Roe, Anne & George Gaylord Simpson (editors). 1958. Behavior and evolution. (Symposium). Yale Univ. Press., New Haven. viii + 557 pp., figs. & tables. $10.00.

Romer, Alfred Sherwood. 1959. The vertebrate story. 4th ed. Univ. Chicago Press., Chicago; Cambridge Univ. Press, London; & Univ. Toronto Press, Toronto. vii + 437 pp., num. figs. $7.00.

Specht, R. L. & C. P. Mountford (editors). 1958. Records of the American-Australian scientific expedition to Arnhem Land. 3. Botany and plant ecology. (Symposium). Melbourne Univ. Press, Carlton; Cambridge Univ. Press, London & New York. xv + 522 pp., figs. & tables. $19.50.

Stirton, Ruben Arthur. 1959. Time, life, and man; the fossil record. John Wiley & Sons., Inc., New York; Chapman & Hall, Ltd., London. xi + 558 pp., 291 figs. $9.00.

UNESCO. 1956. Utilization of saline water; reviews of research. (Symposium). 2nd ed. Arid Zone Research **4**: 1-102, figs. UNESCO, Paris; Columbia Univ. Press, New York.

UNESCO. 1957. Human and animal ecology; reviews of research. (Symposium, bilingual English and French). Arid Zone Research **8**: 1-244, figs. UNESCO, Paris; Columbia Univ. Press, New York.

UNESCO. 1957. Guide book to research data for arid zone development. (Symposium, edited by B. T. Dickson). Arid Zone Research **9**: 1-191 pp., figs. UNESCO, Paris; Columbia Univ. Press, New York.

UNESCO. 1958. Climatology; reviews of research. (Symposium). Arid Zone Research **10**: 1-190, figs. UNESCO, Paris; Columbia Univ. Press, New York. 1.950 fr., $6.50.

UNESCO. 1958. Climatology and microclimatology; proceedings of the Canberra Symposium. (Bilingual English and French). Arid Zone Research **11**: 1-355 pp., figs. UNESCO, Paris; Columbia Univ. Press, New York. 3.300 fr., $11.00.

UNESCO. 1958. Study of tropical vegetation; proceedings of the Kandy Symposium. (Bilingual English and French). Humid Tropics Research [**1**]: 1-226 pp., figs. UNESCO, Paris; Columbia Univ. Press, New York. $3.00.

UNESCO. 1958. Problems of humid tropical regions. (Symposium, bilingual English and French). Humid Tropics Research [**2**]: 1-102 pp., figs. UNESCO, Paris; Columbia Univ. Press, New York. $6.00.

Walker, Edmund M. 1958. The Odonata of Canada and Alaska. Vol. 2, Part 3: The Anisoptera—four families. Univ. Toronto Press, Toronto; Oxford Univ. Press, London. xi + 318 pp., 64 figs., taxonomic keys. $13.00.

***Went, Frits W. et al.** 1957. The experimental control of plant growth; with special reference to the Earhart Plant Research Laboratory at the California Institute of Technology. Chronica Botanica, Vol. **17**. xvii + 343 pp., 71 figs., 25 plates, 21 tables. Chronica Botanica Co., Waltham, Mass. $8.50.

Wieser, Wolfgang. 1959. Free-living nematodes and other small invertebrates of Puget Sound beaches. Univ. Washington Publ. in Biology, Vol. **19**: 1-179, num. figs. Univ. Washington Press, Seattle. $4.00.

* Assigned for review.

CORRECTION

In the paper "Underwater sounds produced by males of the blennid fish *Chasmodes bosquianus*" by W. N. Tavolga, Ecology 39(4), 1958, on p. 759, column 2, fourth line from the bottom, and on page 760, column 2, line 7, "0.5 to 0.8 microbars" should read "0.005 to 0.008 microbars."

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